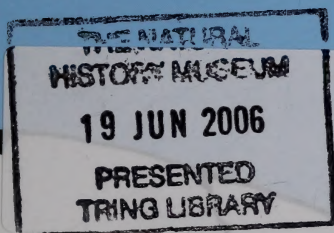
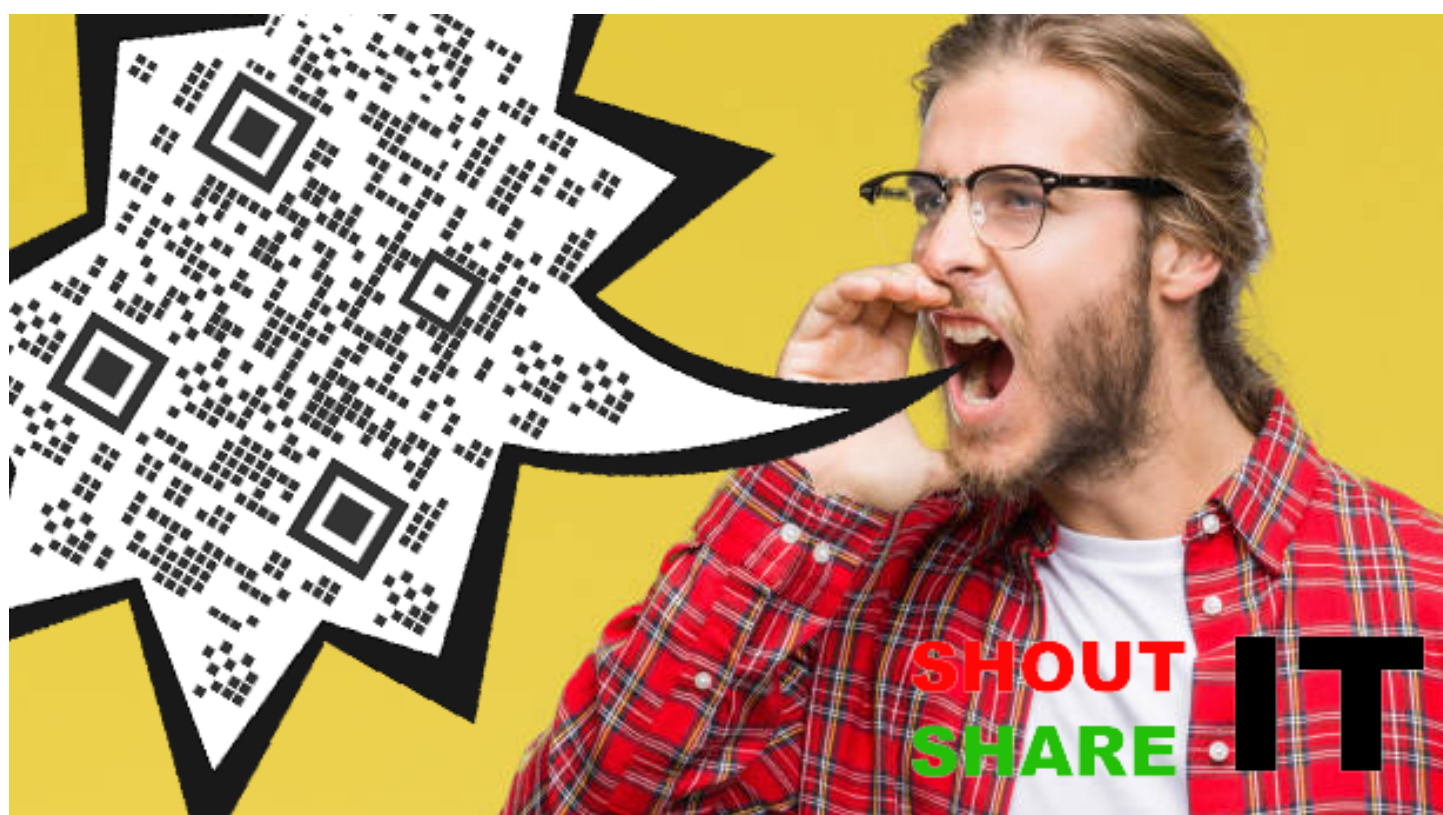


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Recent Avian Extinctions
Edited by Guy M. Kirwan



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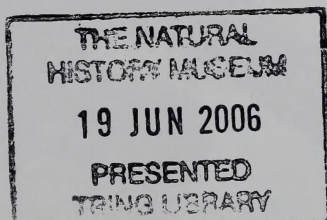
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Recent Avian Extinctions

Papers from a conference of this title
organised by the British Ornithologists' Union,
and supported by the British Ornithologists' Club
and Linnaean Society of London,
held at the Linnean Society of London offices,
on 1 November 2004

Edited by Guy M. Kirwan





Frontispiece. Recently extinct passerines from the Hawaiian island of Oahu, from top to bottom: Akepa *Loxops coccineus rufa* (extinct 1893), Oahu Thrush *Myadestes oahensis* (extinct 1825), Nukupu'u *Hemignathus lucidus lucidus* (extinct c.1860), Ou *Psittirostra psittacea* (extinct c.1900) Akialoa *Hemignathus lichtensteini* (extinct 1837) and Oo Moho *apicalis* (extinct 1837) (Julian Pender Hume)

Recent Avian Extinctions

by *Julian Hume*

The idea for a one-day conference on recent avian extinctions in conjunction with the Linnaean Society of London was originally proposed by Chris Feare. The conference was to comprise a presentation of related topics from researchers working on predominantly Holocene extinctions, particularly as we enter an era of increasingly catastrophic worldwide extinction events. Chris unfortunately had to withdraw at an early stage and I was presented the opportunity to guide the project through to completion. My aim therefore was to organise an international one-day symposium that reflected the present diverse and multi-disciplinary approach to avian research including natural extinction events, DNA, statistical analysis and evidence derived from morphological and historical studies.

In planning, the conference was mainly constructed to encourage discussion and possible scientific collaboration. The choice of papers was biased towards oceanic islands, as evidence derived from the palaeontological record indicates that hundreds, if not thousands, of island bird species have disappeared in recent historic times, nearly all as a result of anthropogenic activity (e.g. Steadman 1995). Therefore, a conference dealing exclusively with recent avian extinctions provided an ideal opportunity to present an overview of research ranging from case studies of species to methods of identifying the scope of extinction events. As a result, I hope that these proceedings highlight the importance of obtaining data through a number of disciplines, and emphasise the fact that biogeographic conclusions based on current diversity and distribution of both oceanic island and, increasingly, continental birds is very much an artefact of human interference.

This conference would not have taken place had it not been for the commitment of Steve Dudley, of the British Ornithologists' Union (BOU), the British Ornithologists' Club (BOC) and the Linnaean Society of London. In particular the BOU provided logistical and administrative expertise and the Linnaean Society their support and premises for the occasion. I am also indebted to the BOC, who funded both this supplement and the colour artwork included within. I further thank Guy Kirwan and Robert Prŷs-Jones for their assistance during the composition of this publication, and all of the speakers/attendees who made the day such a memorable one. Finally, I take this opportunity to dedicate these proceedings to the late Prof. Janet Kear, whose passion and commitment to avian research was unprecedented. Janet co-authored a paper for the conference but sadly, due to ill health, could not personally attend the meeting, and passed away a short time after.

Reference:

Steadman, D.W. 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. *Science* 267: 1123–1131.

New Zealand's extinct giant eagle

by Michael Bunce & Richard N. Holdaway

Since Richard Owen described the first moa (*Dinornithidae*) bone in 1839 the extinct avifauna of New Zealand has continued to offer biological 'surprises'—the Haast's Eagle *Harpagornis moorei* is no exception. A fact about New Zealand still not widely appreciated is that before human occupation it had no native mammals (other than three species of bat)—therefore its flora and fauna evolved in ways very different to those seen in other ecosystems. In terms of a place to research recent avian extinctions, New Zealand offers a good case study—50% of the nearly 250 bird species (present 1,000 years ago) are now extinct. The bones of these extinct taxa can be found in caves and swamp deposits throughout New Zealand—and this excellent avian fossil record extends well into the last glacial period (30,000 years bp). The relatively cool climate has meant that the bones, and the DNA in them, are well preserved. Advances in ancient DNA techniques in the last decade have provided new avenues of research that enable us to investigate the genetic legacy of extinct birds like the Haast's Eagle.

Bones of the Haast's Eagle were first discovered by Julius Haast (founder and first director of the Canterbury Museum) during excavations of the Glenmark swamp in 1871. Haast recognised immediately that this was a huge raptorial bird (modern estimates are 10–14 kg and a wingspan of up to 3 m) that exceeded the size of any extant eagle by some margin. Relatively little research was conducted on the eagle in the ensuing 100 years, but its sheer size fuelled speculation regarding the species' life history, whether it flew and its diet. In the 1990s it was realised that punctures in the pelvis of moa collected years before perfectly matched the size and spacing of the Haast's Eagle talons (Fig. 1a, p.6). Moa up to 200 kg in weight were targets for this predator—the bones show that the eagle struck from the side with considerable force, gripped the moa's pelvic area with one foot, and killed with a single strike by the other foot to the neck or head (Fig. 1). The eagle's extinction (c.500 years ago) was closely tied to the demise of the moa. Rock art, Maori oral history and bone artefacts prove early Polynesians coexisted with the eagle, but there is no evidence that humans were targets for this aerial predator.

Much of New Zealand's avifauna has relatives in Australia—that of Haast's Eagle was long suspected to be the large (4.5 kg, 2 m wingspan) Wedge-tailed Eagle *Aquila audax*—which seemed a good analog because it had been known to attack young emus *Apteryx*—large flightless birds that are distantly related to moas. An exploratory skeletal analysis, using representative genera within the *Accipitridae* (but lacking any Australasian representative of the genera *Hieraaetus*), placed Haast's Eagle as sister to the Wedge-tailed Eagle. However, shifts in body size are common in island ecosystems and may distort skeletal characters used in phylogenetic reconstructions.

To investigate the genetic history of this fascinating raptor we sampled two eagle bones (c.3,000 years old) from the collections of the Museum of New Zealand Te Papa Tongawera. With only 70 or so individuals ever found and only two relatively complete skeletons in existence these are rare bones, making us grateful to the museum for permitting us to destructively sample their collection. The preliminary gene sequences were so different from our original expectations that we initially questioned their authenticity. These data indicated that Wedge-tailed Eagle was only distantly related to Haast's Eagle, which was in fact related to some of the world's smallest eagles—the Little Eagle *Hieraetus morphnoides* from Australia and New Guinea, and the Eurasian Booted Eagle *H. pennatus*, which typically weigh less than 1 kg. Even more striking was how closely genetically related the eagle species were (1.25% difference in their mitochondrial cytochrome-*b* gene). In accordance with a conservative molecular clock, we estimate that their common ancestor lived c.1 MYA. These data suggests an eagle arrived in New Zealand and increased in weight by 10–15 times during this period. This spectacular evolutionary change illustrates the potential speed of size alteration within lineages of vertebrates, especially in island ecosystems.

The question remains as to what environmental/ecological factors drove the eagle to the upper limits for powered (flapping) flight from an ancestor that was likely one-tenth its size? Answering questions concerning the life history of extinct megafauna is akin to guesswork, but we speculate that size of available prey and the absence of other large predators were key in driving the size increase—after killing a moa, the eagle could have fed unhindered and perhaps remained at a kill site for days.

The DNA phylogeny we constructed from 16 extant eagle species demonstrated considerable problems with the current classification of 'booted' eagles (those with feathered tarsi), especially within the genera *Aquila*, *Hieraetus* and *Spizaetus* which are clearly paraphyletic. Assignment of species limits within these genera has traditionally been problematic, making our observation expected. However, it is apparent the name for the extinct New Zealand Eagle should be amended to *Hieraetus moorei*.

In summary, ancient DNA represents a valuable means by which to study the genetic history of extinct fauna, but is only one piece of the puzzle in unravelling their life history. An integrated approach combining DNA, stable isotopes, morphological analysis and other technologies represents the only way to investigate the multitude of other questions concerning extinct fauna, e.g. how large was the population of Haast's Eagle?

A fully referenced research paper is available for free download from the PLoS biology website, www.plosbiology.org.

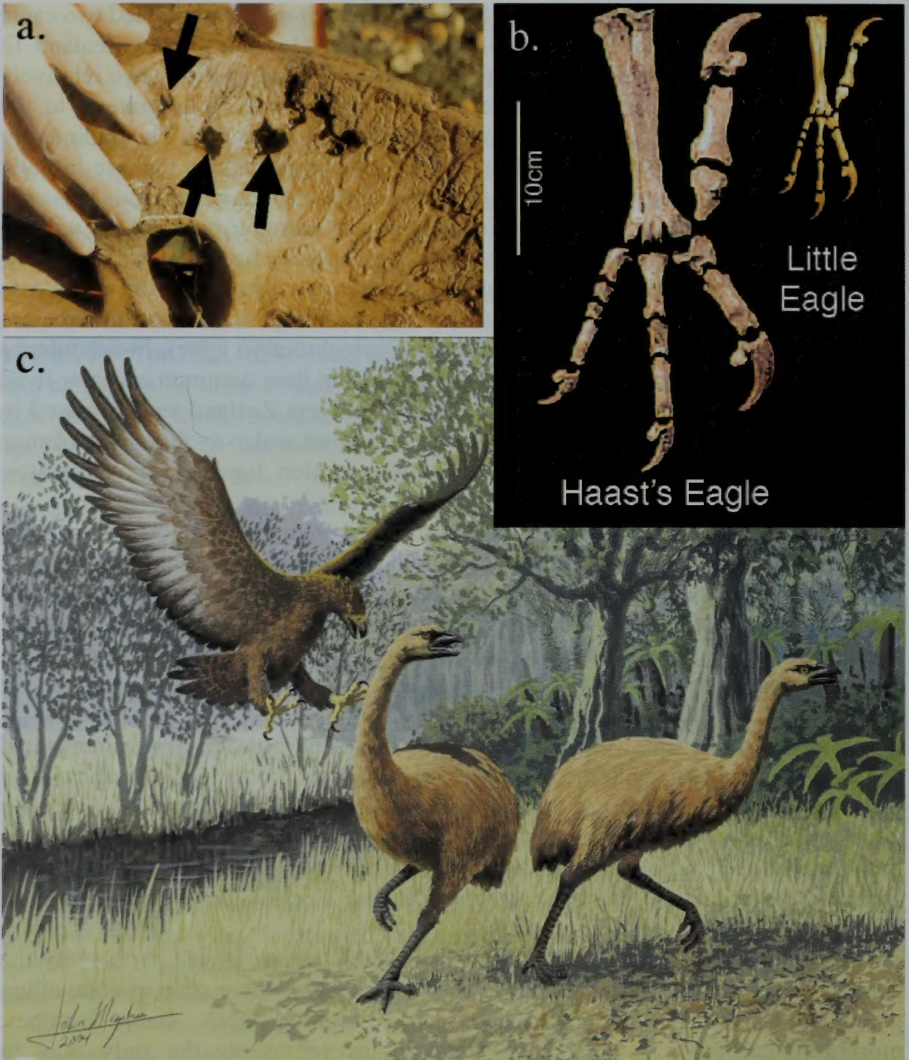


Figure 1. New Zealand's extinct Haast's Eagle *Hieraaetus moorei* (formerly *Harpagornis moorei*). (A) moa pelvis showing puncture marks (marked by arrows) caused by an eagle strike. Evidence of eagle strikes are preserved on skeletons of moa (*Dinornithidae*) weighing up to 200 kg (Trevor Worthy). (B) A direct comparison of the claws of Haast's Eagle with those of its closest known relative, Little Eagle *Hieraaetus morphnoides*, demonstrating the extent of the size change. (C) Artist's impression of Haast's Eagle attacking the extinct New Zealand moa. The eagle struck and gripped the moa's pelvic area (A), and then killed with a single strike of the other foot to the head or neck (John Megahan)

Going or gone: defining 'Possibly Extinct' species to give a truer picture of recent extinctions

by S. H. M. Butchart, A. J. Stattersfield & T. M. Brooks

The IUCN Red List is widely regarded as the most authoritative classification of species by their extinction risk (Lamoreux *et al.* 2003, Hamblen 2004, Rodrigues *et al.* 2006), including those species known to have become extinct in recent times. Birds are the best-documented class of organisms on the Red List, and the fourth complete assessment of the status of the world's birds was recently published (BirdLife International 2004, IUCN 2004), and updated (at www.birdlife.org) for the 2005 IUCN Red List. As well as 1,208 threatened bird species in the categories of Critically Endangered, Endangered and Vulnerable (in order of decreasing risk of extinction), it lists 131 species as having become Extinct since 1500 (for which 'there is no reasonable doubt that the last individual has died': IUCN 2001), and an additional four species as Extinct in the Wild ('known only to survive in captivity': IUCN 2001).

However, extinction—the disappearance of the last individual of a species—is very difficult to detect (Diamond 1987). For a species to be listed as Extinct requires that exhaustive surveys have been undertaken in all known or likely habitat throughout its historic range, at appropriate times (diurnal, seasonal, annual) and over a timeframe appropriate to its life cycle and life form (IUCN 2001). Listing as Extinct has significant conservation implications, because conservation funding is, justifiably, not targeted at species believed extinct. Following a precautionary approach, conservationists are therefore reluctant to designate species as Extinct if there is any reasonable possibility that they may still be extant, in order to avoid the 'Romeo Error' (Collar 1998), where we might give up on a species before it is too late. This term was first applied to the case of Cebu Flowerpecker *Dicaeum quadricolor*, which was rediscovered in 1992 after 86 years without a record (Dutson *et al.* 1993), having been written off as extinct at least 40 years earlier on the presumption that no forest remained on the island of Cebu (Magsalay *et al.* 1995). This remarkable rediscovery is by no means unique. For example, Jerdon's Courser *Rhinoptilus bitorquatus* was rediscovered in 1986 also after 86 years without a record (Bhushan 1986). Caerulean Paradise-flycatcher *Eutrichomyias rowleyi* was known only from the 1878 type specimen and a belatedly published sight record in 1978, with fruitless searches in 1985–86 (Whitten *et al.* 1987) prior to its rediscovery in 1998 (Riley & Wardill 2001).

On the other hand, for some Critically Endangered species the chances of rediscovering a population must be extremely low, and in all probability they are already extinct. For example, Alaotra Grebe *Tachybaptus rufolavatus* underwent a well-documented decline owing to incidental mortality in monofilament gill-nets and predation by introduced carnivorous fish, compounded by hybridisation with Little Grebe *T. ruficollis*. The last confirmed records were in 1985, with individuals

showing some characters of the species seen in 1986 and 1988 (Hawkins *et al.* 2000). The species was near-flightless and restricted to the Lake Alaotra area. There is a slim chance that individuals could survive at Lake Amparihinandriambavy, where unidentified grebes were seen in 2000, but this species is in all probability now extinct (BirdLife International 2004). Similarly, Nukupu'u *Hemignathus lucidus* is endemic to the Hawaiian Islands where it has not been recorded since 1995–96 despite extensive effort in a large proportion of the historic range (Pratt *et al.* 2001). It is in all likelihood extinct as a result of habitat loss and degradation combined with introduced diseases such as avian malaria spread by introduced mosquitoes.

A precautionary approach by IUCN to classifying extinctions is appropriate in order to encourage continuing conservation efforts until there is no reasonable doubt that the last individual of a species has died. It also minimises the danger of 'crying wolf' and reducing confidence in the accuracy of the label Extinct. However, this approach biases analyses of recent extinctions based only on those species officially classified Extinct or Extinct in the Wild. For example, the number of recent extinctions documented on the IUCN Red List is likely to be a significant underestimate, even for well-known taxa such as birds. In recognition of this, we develop a framework to examine relevant evidence and judge as objectively as possible which Critically Endangered species are likely to be already extinct. Using data on these species and on species evaluated as Extinct and Extinct in the Wild, we re-analyse recent extinctions to provide a more realistic assessment of their rate, taxonomic distribution, geography and causes.

Methods

Information on Extinct, Extinct in the Wild, and Critically Endangered species were taken from BirdLife International (2004), updated at www.birdlife.org. The accounts for Extinct species in BirdLife International (2004) were based largely on those in Brooks (2000). Dates were assigned to extinctions and possible extinctions based on the date of the last reliable or confirmed record. In cases for which extinction was estimated to have occurred during a particular period, the midpoint was taken. In theory, more sophisticated techniques for estimating extinction dates are available (Solow 1993), but these require knowledge of the dates of multiple records of a species prior to its extinction, which are rarely available for extinct birds. Recognising that it is difficult in most cases to precisely date extinctions, we analysed temporal patterns by pooling data into 25- or 50-year intervals. We analysed the taxonomy of recent extinctions at the family level, using binomial one-tailed tests to compare the significance of differences between the percentages of extinct species per family with the percentage for the class Aves. Causes of extinction and threats to extant threatened species were coded according to a standard classification of threats used to document all threatened species on the IUCN Red List (http://www.redlist.org/info/major_threats.html). For the purposes of the analyses here, threats deriving from alien invasive species impacting the

habitat of a threatened or extinct species were pooled with other forms of threat by invasive species, rather than with other forms of habitat degradation. For the comparison of extinct and extant threatened species, we considered for the latter only high and medium-impact threats, i.e. those that affect the majority of the population and cause rapid declines (BirdLife International 2004).

Defining ‘Possibly Extinct’ species

We defined ‘Possibly Extinct’ species as those that are, on the balance of evidence, likely to be extinct, but for which there is a small chance that they may be extant and thus should not be listed as Extinct until adequate surveys have failed to find the species and local or unconfirmed reports have been discounted. ‘Possibly Extinct in the Wild’ correspondingly applies to such species known to survive in captivity.

For each species we considered five main types of evidence for extinction:

- For species with recent last records, the decline has been well documented.
- Severe threatening processes are known to have occurred (e.g. extensive habitat loss, the spread of alien invasive predators, intensive hunting, etc.).
- The species possesses attributes known to predispose taxa to extinction, e.g. natural rarity and/or tiny range (as evidenced by paucity of specimens relative to collecting effort), flightlessness, allospecies or congeners that may have become extinct through similar threatening processes, etc.
- Recent surveys have been apparently adequate given the species’ ease of detection, but have failed to detect the species.

We considered four types of evidence against extinction:

- Recent field work has been inadequate (any surveys have been insufficiently intensive/extensive, or inappropriately timed; or the species’ range is inaccessible, remote, unsafe or inadequately known).
- The species is difficult to detect (it is cryptic, inconspicuous, nocturnal, nomadic, silent or its vocalisations are unknown, identification is difficult, or the species occurs at low densities).
- There have been reasonably convincing recent local reports or unconfirmed sightings.
- Suitable habitat (free of introduced predators and pathogens if relevant) remains within the species’ known range, and/or allospecies or congeners may survive despite similar threatening processes.

By explicitly laying out and classifying evidence for and against extinction under this framework, we then judged where to place each species on a continuum from high to low confidence of extinction, on a spectrum from Extinct to Critically Endangered (Possibly Extinct) to Critically Endangered. For any given balance of evidence, the position on this continuum was influenced by the time since the last

confirmed record (see Fig. 1). For example, for species with recently confirmed records to be placed at the Extinct end of the spectrum, there had to be greater confidence in the extinction, i.e. greater confidence in the adequacy of surveys, the absence or inadequacy of local/unconfirmed records, greater severity of threatening processes, and better documentation of, and confidence in, observed population declines. In contrast, species that had not been recorded for many decades (e.g. more than 100 years) were judged to be more likely to have become extinct for a given balance of evidence for and against extinction, owing to the sheer length of time without records. Deciding the strength of evidence for and against extinction is necessarily subjective. However, this framework helped to make these judgements as objective as possible, by setting out the evidence, and weighing this against the time since the last confirmed record.

We tested this framework on 40 Critically Endangered bird species that we considered candidates for Possibly Extinct status. This included all species for which there was any reasonable possibility that they might be extinct, including any that had not been seen for >10 years (despite reasonable searches and/or for which there was a plausible threatening process), and any that had been last seen <10 years

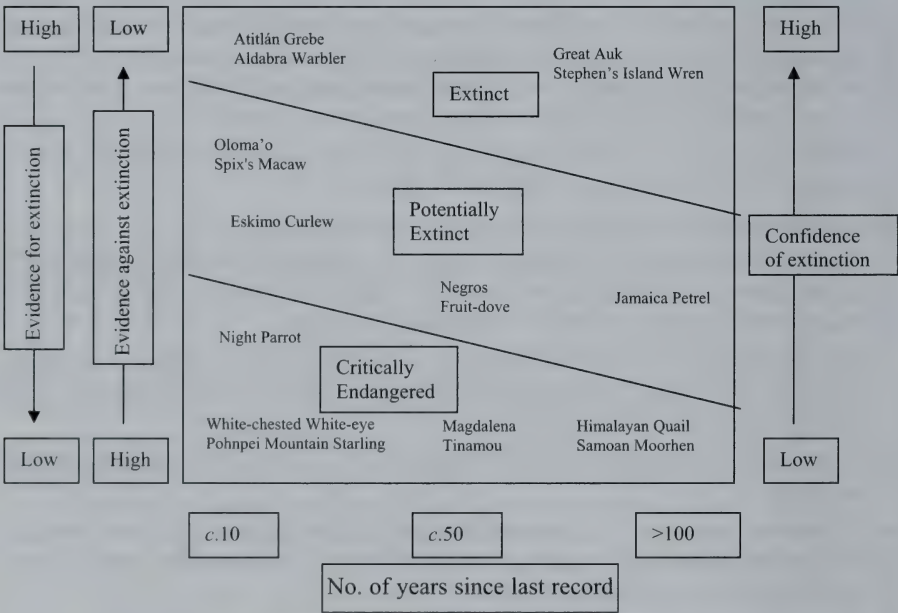


Figure 1. Schematic showing, with selected examples, how time since last record interacts with confidence of extinction to determine how species are classified as Critically Endangered, Possibly Extinct or Extinct. For species last recorded quite recently there needs to be greater confidence that the last individual has died in order for the species to be placed at the extinct end of the spectrum from Critically Endangered to Extinct.

ago for which there had been a well-documented decline of a tiny population. Of these, we identified 15 as Possibly Extinct (including one Possibly Extinct in the Wild species; Appendix 1) and 25 as Critically Endangered (Appendix 2).

One-third of the Possibly Extinct species have not been recorded for more than 50 years or so, and this significant duration since the last records is, of itself, strong evidence that these species may well be extinct. For example, Hooded Seedeater *Sporophila melanops* is known only from the type specimen collected over 180 years ago (BirdLife International 2004). Although habitat destruction in the region of the type locality has not been exceptionally severe, the sheer duration of time without records of a species that could be expected to be relatively easily identified and detected can be considered strong evidence that the species is now extinct. Similarly, Guadalupe Storm-petrel *Oceanodroma macrodactyla* has not been recorded since 1912 despite several searches, following a severe decline owing to predation by introduced cats and habitat degradation by introduced goats (BirdLife International 2004). Only the difficulty of detecting storm-petrels at their breeding colonies at night (when the birds are active) and the continued survival of other storm-petrels on the island point to the possibility that some individuals survive (and hence that classification as Extinct would be premature).

The remaining Possibly Extinct species have undergone well-documented declines, with the most recent records in the last 25 years or so. For example, the last known Spix's Macaws *Cyanopsitta spixii* were monitored until the last individual disappeared in 2000, following a severe decline owing to unsustainable and intensive exploitation for the cagebird trade (Juniper 2003). Searches have not led to the discovery of any other populations, although it is conceivable, if unlikely, that further individuals survive. Similarly, the last well-documented sighting of Oloma'o *Myadestes lanaiensis* was in 1980, with an unconfirmed report in 1988, and there have been no subsequent records despite further surveys in most of the historical range. It is likely to have been driven extinct by disease spread by introduced mosquitoes, and as a result of habitat destruction (Reynolds & Snetsinger 2001). However, the remote Oloku'i Plateau has not been surveyed recently and could still harbour some birds.

Three Vulnerable species have not been recorded for many years, but in each case the threats to them are less intense, and the lack of records clearly results from a lack of surveys, taxonomic uncertainties and/or identification difficulties, rather than because of possible extinction. They are classified as Vulnerable rather than Critically Endangered owing to their presumed small (rather than tiny) and declining populations. The species are: Nicobar Sparrowhawk *Accipiter butleri* (last definite record 1901; possible sightings in the 1990s, but identification uncertain owing to confusion with Besra *A. virgatus*); Manipur Bush-quail *Perdica manipurensis* (last definite record 1932; possible record in 2004, and cessation of hunting, lack of field work and difficulty of detecting this species are likely to explain the lack of records); and Black-browed Babbler *Malacocincla perspicillata* (known only from a specimen collected in 1843–48, but the lack of subsequent

records is most likely to have been a result of confusion over its taxonomic status). In addition, three Endangered species have also not been recorded recently, but are regarded as likely to be extant for similar reasons. They are classified as Endangered on the basis of their small known ranges and because their remaining populations are assumed to be too large to qualify as Critically Endangered. They are: Recurve-billed Bushbird *Clytactantes alixii* (last recorded 1965 despite recent searches, but known from several sites in north Colombia and north-west Venezuela), Chestnut-bellied Flowerpiercer *Diglossa gloriosissima* (last recorded in 1965, but there has been a dearth of recent field work within its known range in Colombia), and Táchira Antpitta *Grallaria chthonia* (last recorded 1956 despite recent searches, but suitable habitat remains within the large national park in Venezuela from which the species is known).

We also examined a number of Data Deficient species that have not been recorded for many years. Data Deficient is a category on the IUCN Red List applied to species for which 'there is inadequate information to make a direct or indirect assessment of [the] risk of extinction' (IUCN 2001). For six species (Cayenne Nightjar *Caprimulgus maculosus*, Vaurie's Nightjar *C. centralasicus*, White-chested Tinkerbird *Pogoniulus makawai*, Red Sea Swallow *Hirundo perditia*, Sillem's Mountain-finch *Leucosticte sillemi* and Black-lored Waxbill *Estrilda nigriloris*) the available evidence suggests that they are unlikely to be threatened (and hence unlikely to be near extinction or potentially extinct), because no threatening factor is known or can be inferred, and there are convincing practical reasons for the lack of recent records (e.g. surveys have been inadequate, the species is difficult to detect and/or there is taxonomic uncertainty). In three cases (Sharpe's Rail *Gallirallus sharpei*, Coppery Thorntail *Popelairia letitiae* and Bogotá Sunangel *Heliangelus regalis*) knowledge of the original range is so poor that no further inferences can be made (e.g. Sharpe's Rail is known from an 1893 specimen of unknown provenance, possibly from the Greater Sundas).

The 15 species we identified as Possibly Extinct will be tagged as such on the IUCN Red List. The framework developed here is currently being tested on amphibians and mammals, prior to being considered, with potential modifications, for general adoption by the IUCN Red List.

Recent extinctions reanalysed

We combined data on Critically Endangered (Possibly Extinct), Extinct and Extinct in the Wild species from BirdLife International (2004; updated at www.birdlife.org) to undertake a realistic analysis of the pattern of recent extinctions.

Extinction rates

Combining totals for Extinct (131), Extinct in the Wild (four) and Critically Endangered (Possibly Extinct) species (15), exactly 150 bird species have gone or are likely to have become extinct since 1500. This represents a rate of 0.30 species per year. Since 1900, the total is 59 species: 0.56 species per year. While these data

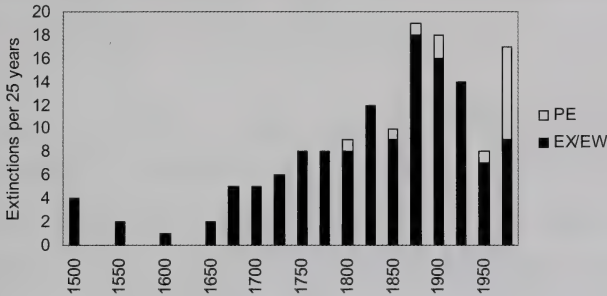


Figure 2. Number of avian extinctions per 25-year period showing totals for Critically Endangered (Possibly Extinct) species ('PE'; $n=15$), and Extinct ('EX'; $n=131$) plus Extinct in the Wild ('EW'; $n=4$) species.

may underestimate the extinction rate of 500 years ago, because some species may have become extinct without our knowledge (Balmford 1996), it appears that the extinction rate increased rapidly from the late 1600s, and peaked in the late 1800s and early 1900s at 0.72 species p.a. (in 1875–1925; Fig. 2). Very recent extinction rates remain high: 17 species were lost in the last quarter of the 20th century, and two species since 2000. The last known individual of Spix's Macaw *Cyanopsitta spixii* (Critically Endangered [Possibly Extinct in the Wild]) disappeared in Brazil in late 2000, and the last two known individuals of Hawaiian Crow *Corvus hawaiiensis* (Extinct in the Wild) disappeared in June 2002. Po'ou-uli *Melamprosops phaeosoma*, also from the Hawaiian Islands, looks set to become the next addition to this list: one of the last three known individuals was taken into captivity in September 2004 but died two months later, and the other two individuals have not been seen for over a year (K. Swynnerton *in litt.* 2004). Fig. 2 shows clearly how important it is to consider Possibly Extinct species in assessing recent extinction rates: the total number of estimated extinctions in the last quarter of the 20th century almost doubles from nine to 17 when Possibly Extinct species are included.

How do these extinction rates compare to those derived from the fossil record? Comparisons of absolute rates are difficult given considerable uncertainty over the total number of species on the planet, so it is useful to compare relative extinction rates, expressed as extinctions per million species per year (E/MSY; Pimm *et al.* 1995). Mean fossil species lifetimes produce a background extinction rate of 0.1–1 E/MSY. The total number of bird extinctions since 1500 (150/9,906 species) therefore equates to 30–300 times the background rate. Taking the number of extinctions since 1900 (59/9,815 extant species in 1900) gives an extinction rate 57–570 times background extinction rates. These are still highly conservative estimates for the extinction rate across all taxa, because many taxonomic groups (e.g. amphibians, fish, plants, invertebrates) have on average much smaller ranges, and hence likely higher extinction rates in the face of human impact than do birds.

Estimates of extinction rates derived from measurement of a range of extinction drivers (e.g. habitat destruction, human energy consumption) yield E/MSY 1,000–11,000 higher than background rates (Pimm & Brooks 1999).

Geography of recent extinctions

Recent avian extinctions have occurred across the world, with particularly large numbers in Hawaii (27), Mauritius (18), New Zealand (14), Réunion (11) and St Helena (nine; Fig. 3). The majority (89.3%) has been on islands even though most bird species (>80%) live on continents (Johnson & Stattersfield 1990, Manne *et al.* 1999). However, continental species have been far from immune, and those subject to extinction often originally had extensive ranges. The wave of extinctions on islands may be slowing, perhaps because many of the potential introductions of alien species to predator-free islands have already occurred, and because so many susceptible island species are already extinct. By contrast, the rate of extinctions on continents appears to be sharply increasing (Fig. 4) owing to extensive and expanding habitat destruction (see below).

Taxonomy of recent extinctions

Recent extinctions have not been random with respect to taxonomy. Thirteen families were found to have suffered significantly more extinctions than expected by chance (Table 1). Among large families, Anatidae (ducks, geese and swans), Rallidae (rails), Psittacidae (parrots) and Sturnidae (starlings) have suffered a disproportionate number of extinctions. The Dromaiidae (emus), Raphidae (Dodo *Raphus cucullatus* and solitaires) and Acanthisittidae (New Zealand wrens) have all lost 50% or more of their species in the last 500 years. Conversely, some families

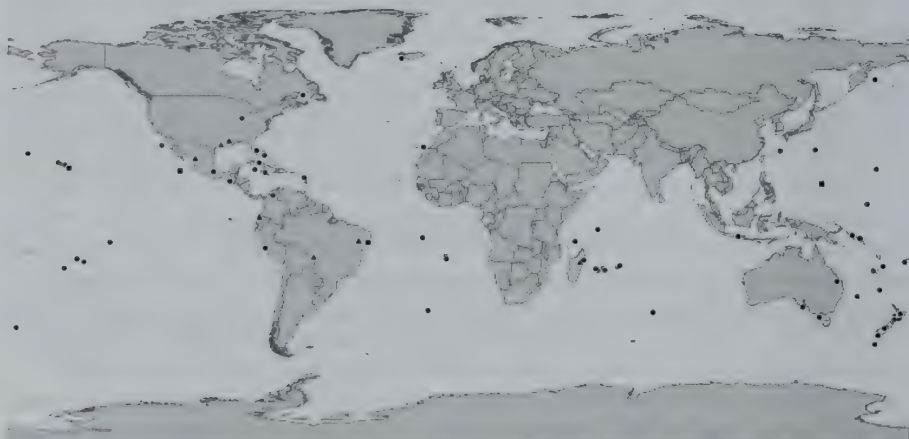


Figure 3. Global distribution of recent avian extinctions. Localities show last known records of Extinct (squares, $n=131$), Extinct in the Wild (circles, $n=4$), and Critically Endangered (Possibly Extinct) species (triangles, $n=15$).

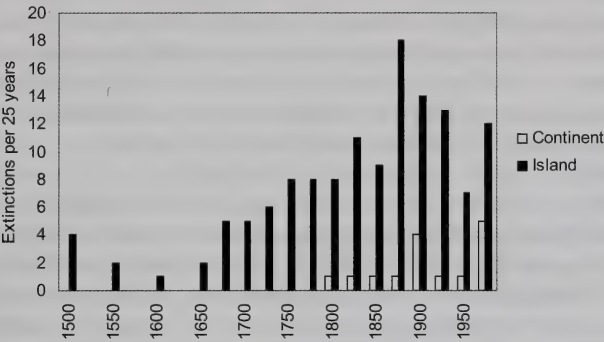


Figure 4. Number of avian extinctions per 25-year period on continents and islands. Totals include Extinct (*n*=131), Extinct in the Wild (*n*=4), and Critically Endangered (Possibly Extinct) species (*n*=15).

(or subfamilies) have suffered significantly fewer extinctions than expected by chance: Accipitridae (hawks and eagles, 0 extinctions/ 239 species), Formicariidae (anthrushes, 0/267), Furnariidae (ovenbirds, 0/242), Tyrannidae (tyrant-flycatchers, 0/409), Muscicapidae (thrushes, babblers, warblers and Old World flycatchers, 12/1,551), Emberizidae (buntings, 1/614; *P*<0.02 in each case). Passerines formed 19% of continental extinctions (3/16 species) and 34% of island extinctions (46/134 species), but this difference is not significant ($\chi^2= 1.58, P=0.21$).

TABLE 1
Families with significantly more recently extinct species (Extinct, Extinct in the Wild, and Possibly Extinct) than expected by chance.

Family	No. species	No. extinct species	% extinct	P
Raphidae (dodo, solitaires)	2	2	100	0.0002
Dromaiidae (emus)	3	2	66.7	0.0007
Acanthisittidae (New Zealand wrens)	4	2	50	0.0014
Drepanididae (honeycreepers)	34	16	47.1	<0.0001
Callaeidae (New Zealand wattlebirds)	3	1	33.3	0.0450
Upupidae (hoopoes)	3	1	33.3	0.0450
Rallidae (rails)	156	23	14.7	<0.0001
Podicipedidae (grebes)	22	3	13.6	0.0044
Ardeidae (herons)	67	4	6	0.0193
Psittacidae (parrots)	374	20	5.3	<0.0001
Sturnidae (starlings)	114	5	4.4	0.0308
Anatidae (ducks, geese, swans)	164	7	4.3	0.0039
Columbidae (pigeons)	318	13	4.1	0.0014

Causes of recent extinctions

Extinction is a natural phenomenon, being the final stage of the evolutionary trajectory that each species follows. However, recent extinctions appear to have been precipitated by human actions, either directly or indirectly. Here we analyse the broad mechanisms by which such extinctions have occurred, as classified on the IUCN Red List (BirdLife International 2004, IUCN 2004).

The impacts of habitat destruction and degradation, alien invasive species and over-exploitation by humans have been the major causes of recent avian extinctions (Fig. 5). Alien invasive species have been a cause of extinction or likely extinction for at least 77 species. Invasive species have impacts in different ways. Most important has been predation: introduced dogs, pigs, mongooses and, in particular, cats and rats have contributed to the extinction of at least 56 species. The most notorious example was the Stephen's Island Wren *Traversia lyalli*, whose entire world population was rapidly wiped out when cats became established on the island in 1894 (Tyrberg & Milberg 1991, Galbreath & Brown 2004). Diseases caused by introduced pathogens have contributed to the extinction of 20 species, 16 of them on Hawaii where introduced avian malaria and avian pox (transmitted by introduced mosquitoes) has had (and continues to have) devastating consequences (Scott *et al.* 1986, van Riper *et al.* 1986, Atkinson *et al.* 1995). Habitat destruction by sheep, rabbits and goats has been implicated in the extinctions of another ten species, and competitors have impacted six species. Gurevitch & Padilla (2004) argued that the evidence for invasive species having contributed to extinctions is poor, and noted that just 2% of 762 species listed as Extinct on the 2003 IUCN Red List were documented as having been impacted by invasive species. Their result contrasts with ours that

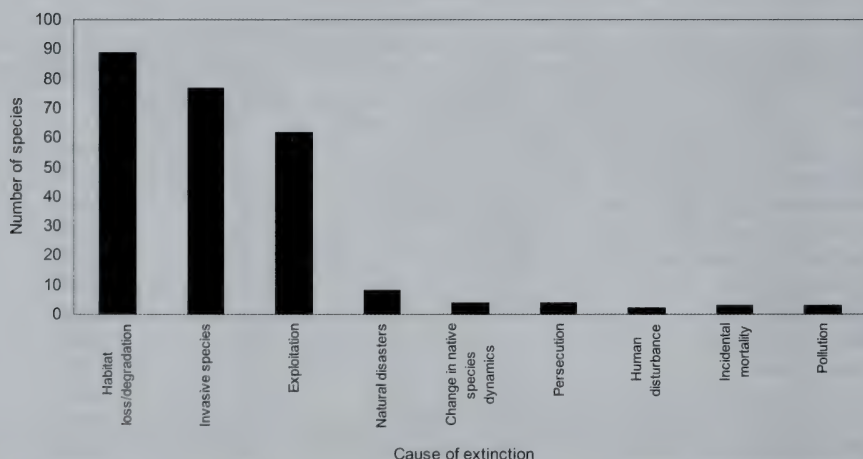


Figure 5. Causes of recent avian extinctions. Totals include Extinct ($n=131$), Extinct in the Wild ($n=4$), and Critically Endangered (Possibly Extinct) species ($n=15$).

invasive species were a major contributory factor to 51% of recent avian extinctions. Blackburn *et al.* (2004) and Clavero & Garcia-Berthou (2005) also provided strong evidence of the importance of invasive species in driving avian extinctions.

It is important to note that many species are impacted by combinations of threats: 48.7% of extinct species have multiple causes of extinction recorded, and this figure is likely to be an underestimate owing to lack of information on historical extinctions.

There are differences in the causes of extinctions of island versus continental species, with habitat loss and exploitation appearing to be more important causes of extinctions on continents than islands, although this result was marginally non-significant (habitat loss: 87.5% vs. 56.0% of species; exploitation: 62.5% vs. 38.1% of species; invasive species: 37.5% vs. 53.0% of species; $\chi^2 = 4.13$, $P = 0.076$; Fig. 6). The apparent reduced importance of exploitation as an extinction driver on islands may be partly explained by the fact that passerines (which, being smaller, are less often targets for hunting) form a substantially lower proportion of island extinctions compared to continental extinctions (see above). It may also be a consequence of an extinction filter effect (Balmford 1996): non-passerine island species susceptible to exploitation through their size and naïveté may have already been driven extinct prior to 1500.

It is interesting to compare the threats to Extinct and Possibly Extinct species with those to extant threatened species (Fig. 7). Whilst habitat loss is the most important factor in both cases (impacting 59.3% of extinct species and 54.6% of threatened species), invasive species and exploitation were much more important as

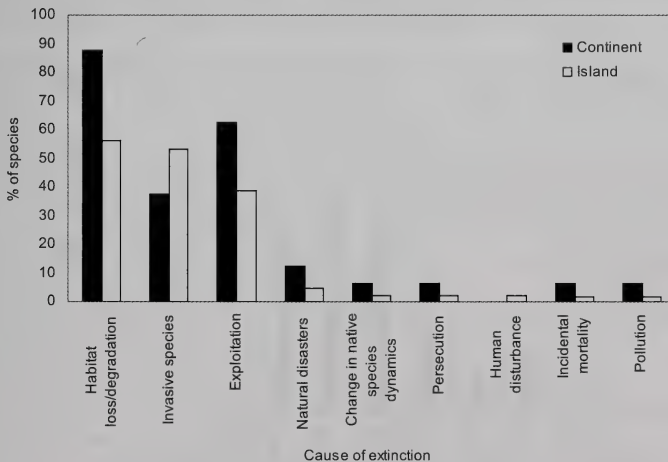


Figure 6. Causes of recent avian extinctions on continents ($n=16$ species) and islands ($n=134$ species). Totals include Extinct ($n=131$), Extinct in the Wild ($n=4$), and Critically Endangered (Possibly Extinct) species ($n=15$).

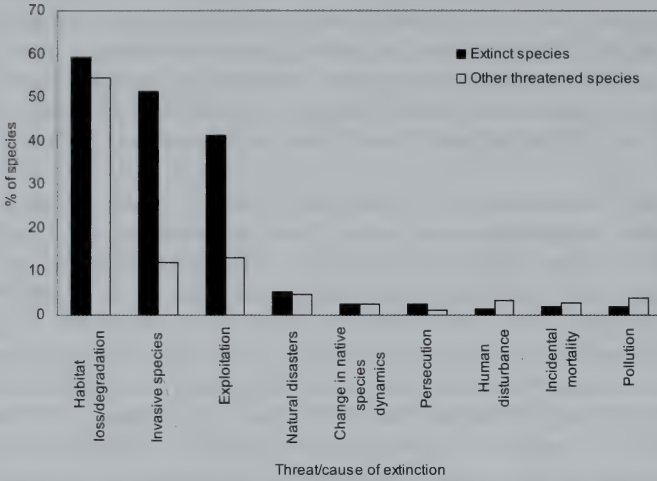


Figure 7. Causes of recent avian extinctions compared to threats to extant threatened birds. Extinct species include Extinct ($n=131$), Extinct in the Wild ($n=4$), and Critically Endangered (Possibly Extinct) species ($n=15$). Other threatened species include those classified as Critically Endangered (excluding Possibly Extinct), Endangered and Vulnerable ($n=1,193$).

causes of extinctions (implicated for 51.3% and 41.3% of species respectively) than as a threat to extant threatened species (12.1% and 13.1% of species respectively). However, as Blackburn *et al.* (2004) pointed out, invasive species (particularly predators) are still a potentially important driver for future extinctions. Most islands currently have few invasive predators: colonisation by additional predators is likely to lead to progressively more extinctions unless prompt intervention is achieved.

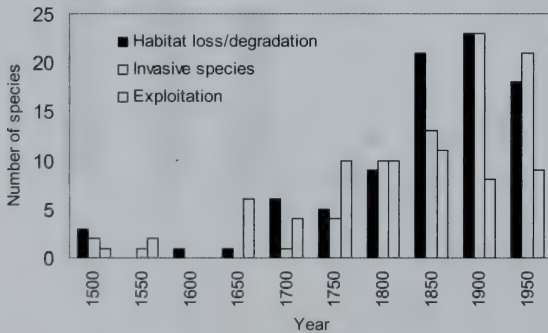


Figure 8. Causes of avian extinctions over time. Totals include Extinct ($n=131$), Extinct in the Wild ($n=4$), and Critically Endangered (Possibly Extinct) species ($n=15$).

Plotting the pattern of the number of extinctions over time caused by the three most important factors (habitat loss/degradation, invasive species and exploitation) shows that the importance of exploitation in driving extinctions has decreased through the 20th century whilst the importance of invasive species and habitat loss and degradation has increased (Fig. 8).

Conclusions

We developed and used the framework presented here to identify 15 Critically Endangered bird species as Possibly Extinct. Combining data on these species with data for 135 Extinct and Extinct in the Wild species shows that over the last century bird species have become extinct at a rate of one every 1.8 years. Habitat loss and degradation, invasive species and exploitation have been the main causes of extinction. Although the vast majority of documented extinctions thus far have been on islands, if we continue to degrade and destroy vast areas of natural habitats then it will be difficult to prevent even more extinctions from occurring imminently on continents.

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APPENDIX 1
Critically Endangered (Possibly Extinct) species, with evidence for and against extinction having occurred.

Species	Evidence for extinction			Evidence against extinction			Notes
	Last confirmed record	Well-documented recent decline	Severe threatening processes	Predisposed to extinction?	Good recent surveys	Inadequate surveys	
Hooded Seed-eater <i>Sporophila melanops</i>	1823					Near type locality.	Habitat destruction around type locality not severe.
Jamaican Parakeet <i>Siphonanthus americanus</i>	1860		Introduced predators; severe habitat loss.				Unidentified nightjar observations may refer to this species.
Jamaica Petrel <i>Pterodroma caribbaea</i>	1879		Introduced predators.				Searches in 1996-2000 failed.
Turquoise-throated Puffleg <i>Eriocnemis godini</i>	<1900		Habitat destroyed at only known locality.	x		Near type locality.	
Guadalupe Storm-petrel <i>Oceanodroma macrodactyla</i>	1912		Predation by feral cats; nesting habitat degraded by goats.			Wrong time of year.	Several searches have failed but Leach's Storm-petrel still survives on island.
Imperial Woodpecker <i>Campephilus imperialis</i>	1956		Habitat loss; hunting.		Conspicuous		Some credible records in 1990s; recent discovery of suitable habitat (though surveys failed) indicates that other such areas may remain.
Eskimo Curlew <i>Numenius borealis</i>	1981	x	Habitat loss & hunting.			x	1990 ?
Oahu Alouahio <i>Paroreomyza maculata</i>	1985	x	Habitat loss; malaria, introduced predators.	Lowland		x	Four apparently reliable reports in Canada in 1987 and unconfirmed reports in Argentina in 1990.

Ou	1987	x	Habitat loss; malaria, introduced predators.			x
<i>Psittirostra psittacea</i>						
Alaotha Grebe	1988	x	Hybridisation; introduced fish; habitat loss.	Flightless?	x	
<i>Tachybaptus rufolavatus</i>						
Oloma'o	1988	x	Habitat loss; malaria, introduced predators.	Lowland	x	x
<i>Myadestes lanaiensis</i>						
Bachman's Warbler	1988	x	Habitat loss.		x	x
<i>Vermivora bachmani</i>						Recent unconfirmed sightings. Incomplete surveys of Congaree Swamp, South Carolina; partial habitat elsewhere.
Madagascar Pochard	1991		Habitat loss; invasive species.		x	
<i>Arthya innotata</i>						
Nukupu'u	1996	x	Habitat loss; malaria, introduced predators.	x		x
<i>Hemignathus lucidus</i>						
Spix's Macaw	2000	x	Trapping; habitat loss.	x	x	Captive populations survive.
<i>Cyanopsitta spixii</i>						

APPENDIX 2

Selected Critically Endangered species not considered to be Possibly Extinct, with evidence for and against extinction having occurred.

Species	Last confirmed record	Evidence for extinction	Evidence against extinction	Notes
Siau Scops-owl <i>Otus siaoensis</i>	1866	Well-documented recent decline Severe threatening processes	Predisposed to extinction? Good recent surveys	Habitat remains
Samoan Moorhen <i>Gallinula pacifica</i>	1873	Introduced predators; hunting.	x	Unconfirmed reports
Himalayan Quail <i>Ophrysia superciliosa</i>	1876	Habitat loss.	x	2003

1890	New Caledonian Rail <i>Porphyrio kukwiedei</i>				Inaccessible, few surveys.	x	1998	x
1891	Sulu Bleeding-heart <i>Gallicolumba menagei</i>	Habitat loss.			x		1995	x
1913	New Caledonian Lorikeet <i>Charmosyna diadema</i>				x		x	x
1918	Rueck's Blue-flycatcher <i>Cyornis ruckii</i>	Habitat destroyed at only known locality.	x		Limited survey work in Sumatran lowlands.	x	x	x
1929	Beck's Petrel <i>Pseudobulweria becki</i>				x		x	x
1931	Silvery Woodpigeon <i>Columba argentina</i>	Habitat loss.			x		2002	x
1943	Magdalena Tinamou <i>Crypturellus saltauarius</i>	Habitat loss.			None in 1940–2000.		1990s	x
1940	Javan Lapwing <i>Vanellus macropterus</i>	Severe habitat loss.		Conspicuous	x		2002	x
1949	Pink-headed Duck <i>Rhodonessa caryophyllacea</i>	Intensive hunting; habitat loss.	x	Conspicuous	Further surveys needed in Myanmar.		2004	x
1955	Archer's Lark <i>Heteromitra archeri</i>	Habitat loss and degradation.		x	Most surveys restricted to type locality.	x	2003	x
1953	Negros Fruit-dove <i>Ptilinopus arcanus</i>	Severe habitat loss.	x	x	Needed on Panay.		2002	x
1961	Semper's Warbler <i>Lecuopeza semperi</i>	Introduced predators.			No intensive searches.		2003	x
1962	Glaucous Macaw <i>Anodorhynchus glaucus</i>	Trapping; habitat loss.		x	Very large former range.		1990s	x
1964	Crested Shelduck <i>Tadorna cristata</i>	Habitat loss.		Conspicuous	Many areas poorly surveyed.		x	x
1974	Makira Moorhen <i>Gallinula silvestris</i>	Introduced predators.	x			x	2002	x

Congeners very inconspicuous.
Presumably low density; inconspicuous.
Reports of *P. rostrata* in Bismarcks/Solomons may refer to this species. Difficult to separate from *Ducula bicolor*.
First surveys in 2002 failed, but some suitable habitat inaccessible.
Searches planned in 2005–06
Unconfirmed sighting in Kachin state, Myanmar, November 2004. Further searches planned.
Species is exceptionally reclusive.
May be montane. Recent convincing local report.
Some habitat remains; several possible sightings.
Persistent unconfirmed reports.
Original range poorly understood. Habitat loss insufficient.
Convincing recent local reports.

Bahia Tapaculo	1983	Severe habitat loss.							
<i>Scytalopus psychopomus</i>									
Liberian Greenbul	1985	Habitat loss.							
<i>Phyllastreptus leucolepis</i>									
White-eyed River-martin	1986	Habitat loss.							
<i>Eurycelidon sirintarae</i>									
Night Parrot	1990								
<i>Geopsittacus occidentalis</i>									
Bulo Burti Boubou	1990								
<i>Laniarius liberatus</i>									
Pohnpei Mountain Starling	1995	Habitat loss, hunting, predation by invasive rats.							
<i>Aplonis pelzelii</i>									
White-chested White-eye	2000	Predation by invasive rats.	x						
<i>Zosterops albogularis</i>									

NOTE ADDED IN PROOF.—Confirming their classification here as Critically Endangered, and not Possibly Extinct, Night Parrot was rediscovered at Mulga Downs, Australia, in 2005 (R. Davis *in litt.* 2006), populations of Bahia Tapaculo have been found at Itubera and Una Biological Reserve, Bahia, Brazil (F. Olmos & P. C. Lima *in litt.* 2006), and White-chested White-eye was seen again as recently as 2004 (P. Olsen & R. Ward *in litt.* 2006). Two Endangered species discussed here have also been recently rediscovered: Recurve-billed Bushbird and Chestnut-bellied Flowerpiercer (O. Laverde, C. J. Sharpe & P. C. Pulgarin *in litt.* 2006).

Taxonomic status has also been questioned. Original range poorly understood. Nocturnal, nomadic. Not seen since described but no subsequent surveys. Taxonomic status has been questioned. Drastic decline since 1930, only one record in last 50 years. In severe decline; formal surveys have failed to find any for 20 years.

The rise and fall of wildfowl of the western Indian Ocean and Australasia

by H. Glyn Young & Janet Kear[†]

Wildfowl (Anseriformes) are amongst the most widespread of vertebrates. Highly volant, dispersive and often long-distance migrants, wildfowl have been recorded on almost every landmass and have colonised many of the world's islands, often radically changing their morphology in the process (Lack 1970, Weller 1980).

The islands of the western Indian Ocean (Madagascar and associated islands, Amsterdam, and the subantarctic islands of Crozet, Kerguelen and St Paul), the Andamans, the Greater and Lesser Sundas, Moluccas, Philippines, New Guinea, Australia and New Zealand (Map 1) lie in three zoogeographical regions (the Malagasy, Oriental and Australasian Regions). However, whilst those wildfowl



Figure 1. Map of islands included in this review.

species found there may have differing evolutionary origins, there is also evidence of a dispersal by colonising ancestral species (notably grey teal and white-eyed pochards) around the region. It is, therefore, not unreasonable to consider these seemingly unrelated islands together for this review of regional colonisation and extinction in wildfowl.

Excluding a small number of migrant wildfowl from Eurasia, and introduced species, 65 taxa are known to have been resident in the region during the Holocene (Table 1). This list includes several taxa known only from subfossil remains (taxonomy and nomenclature of extant taxa is from Kear (2005) and extinct taxa from Livezey (1997) and Holdaway *et al.* (2001): see these publications and Young *et al.* (1996) for extensive reference lists). Of resident taxa, 57 (87%) are endemic to the region but 19 endemic wildfowl taxa (33% of regional endemics) have become extinct during the Holocene. All extinctions are from the Malagasy faunal region, the subantarctic islands and New Zealand; the precise number of extinct taxa from this region is still unknown (e.g. Young *et al.* 1996, Holdaway *et al.* 2001).

Our aim here is to provide a brief overview of the diversity of wildfowl that have colonised the islands of the western Indian Ocean and Australasia, and their decline in recent times. Two taxa considered to have become extinct most recently (Madagascar Pochard *Aythya innotata* and Auckland Islands Merganser *Mergus australis*) are detailed separately.

The rise of wildfowl in the region

Wildfowl have dispersed freely into the region from elsewhere in the world and representatives of most of the popularly recognised groups have colonised the islands. Johnsgard's (1978) proposed system of tribes, whilst now considered overly simplified (see Livezey 1997, Callaghan & Harshman 2005), is still widely used and, of the 13 tribes listed by Johnsgard, members of 12 have been resident in the region in recent times (Table 2).

The exact geographic origins of many of the resident wildfowl are often unclear. Many taxa, especially those in Australasia, have no close living relatives outside the region. Wildfowl are probably southern and tropical in origin (Kear 1970, Callaghan & Harshman 2005) and it is perhaps unsurprising that so many ancient and distinctive taxa are known from the region. For example, the Australian Magpie Goose *Anseranas semipalmatus*, sole member of the Anseranatidae, and New Zealand's river specialist, the Blue Duck *Hymenolaimus malacorhynchos*, which is typically placed in a grouping with the South American Torrent Duck *Merganetta armata* (Callaghan & Harshman 2005), have no obvious relatives anywhere (see Callaghan 2005a). Two further, aberrant, sister genera, *Cnemiornis* (two species) in New Zealand and *Cereopsis* in Australia are related most closely to another curious species, the South American Coscoroba Swan *Coscoroba coscoroba* (St John *et al.* 2005).

New Guinea's Salvadori's Duck *Salvadorina waigiensis* and the Pink-eared Ducks (*Malacorhynchus membranaceus* in Australia and *M. scarletti* in New

TABLE 1

Wildfowl species resident in western Indian Ocean and Australasia. Taxa endemic to region are in bold, extinct taxa are underlined; ▲ taxon resident; □ taxon extinct. NZ New Zealand, AUS Australia, NG New Guinea, PH Philippines, MOL Moluccas, SUND Sundas, AND Andaman and Nicobar Islands, MAD Malagasy Faunal Region (Madagascar, Comores, Seychelles & Mascarene Islands), SUB Subantarctic islands (Amsterdam, Crozet, Kerguelen and St Paul).

Species	NZ	AUS	NG	PH	SUND	MOL	AND	MAD	SUB
Magpie Goose <i>Anseranas semipalmatus</i>		▲	▲						
White-faced Whistling-duck <i>Dendrocygna viduata</i>								▲	
Spotted Whistling-duck <i>Dendrocygna guttata</i>			▲	▲		▲			
Fulvous Whistling-duck <i>Dendrocygna bicolor</i>								▲	
Plumed Whistling-duck <i>Dendrocygna eytoni</i>		▲							
Wandering Whistling-duck <i>Dendrocygna arcuata australis</i>			▲	▲					
<i>Dendrocygna a. arcuata</i>			▲						
<i>Dendrocygna a. pygmaea</i>			▲		▲				
Lesser Whistling-duck <i>Dendrocygna javanica</i>					▲		▲		
White-backed Duck <i>Thalassornis leuconotus insularis</i>								▲	
Musk Duck <i>Biziura lobata</i>		▲							
New Zealand Musk Duck <i>Biziura delatouri</i>	□								
Black Swan <i>Cygnus atratus</i>	□	▲							
Cape Barren Goose <i>Cereopsis n. novaehollandiae</i>		▲							
<i>Cereopsis novaehollandiae grisea</i>		▲							
South Island Goose <i>Cnemidornis calcitrans</i>	□								
North Island Goose <i>Cnemidornis gracilis</i>	□								
Freckled Duck <i>Stictonetta naevosa</i>		▲							
Blue-billed Duck <i>Oxyura australis</i>		▲							
Blue Duck <i>Hymenolaimus malacorhynchus</i>	▲								
African Comb Duck <i>Sarkidiornis melanotos</i>									▲
Greater Madagascan Sheldgoose <i>Centronis majori</i>									□
Lsr. Madagascan Sheldgoose <i>Alopochen sirabensis</i>									□
Mauritius Sheldgoose <i>Alopochen mauritanus</i>									□
Réunion Sheldgoose <i>Alopochen kervazoi</i>									□
Chatham Island Duck <i>Pachyanas chathamica</i>	□								
Radjah Shelduck <i>Tadorna radjah rufitergum</i>		▲							
<i>Tadorna radjah radjah</i>			▲			▲			
Australian Shelduck <i>Tadorna tadornoides</i>		▲							
Paradise Shelduck <i>Tadorna variegata</i>	▲								
Chatham Shelduck <i>Tadorna</i> sp.	□								
Pink-eared Duck <i>Malacorhynchus membranaceus</i>		▲							
Scarlett's Duck <i>Malacorhynchus scarletti</i>	□								
Salvadori's Duck <i>Salvadorina waigiensis</i>			▲						
White-winged Duck <i>Asarcornis scutulata leucoptera</i>					▲				
Australian Wood Duck <i>Chenonetta jubata</i>		▲							
Finsch's Duck <i>Chenonetta finschi</i>	□								
African Pygmy-goose <i>Nettapus auritus</i>									▲
Cotton Teal <i>Nettapus c. coromandelianus</i>				▲	▲	▲			
<i>Nettapus c. albipennis</i>		▲							
Green Pygmy-goose <i>Nettapus pulchelus</i>		▲	▲						

Amsterdam Island Duck <i>Anas marecula</i>						□
St Paul Island Duck <i>Anas</i> sp.						□
Philippine Duck <i>Anas luzonica</i>			▲			
Meller's Duck <i>Anas melleri</i>						▲
Australasian Shoveler <i>Anas rhynchotis</i>	▲	▲				
Madagascar Teal <i>Anas bernieri</i>						▲
Sauzier's Teal <i>Anas theodori</i>						□
Indonesian Teal <i>Anas gibberifrons</i>				▲	▲	
Grey Teal <i>Anas gracilis</i>	▲	▲	▲			
Andaman Teal <i>Anas albogularis</i>					▲	
Chestnut Teal <i>Anas castanea</i>		▲				
Brown Teal <i>Anas chlorotis</i>	▲					
Auckland Island Teal <i>Anas aucklandica</i>	▲					
Campbell Island Teal <i>Anas nesiotis</i>	□					
Macquarie Island Teal <i>Anas</i> sp.	▲					
Red-billed Pintail <i>Anas erythrorhynchos</i>					▲	
Kerguelen Pintail <i>Anas eatoni eatoni</i>						▲
Crozet Pintail <i>Anas eatoni drygalskii</i>						▲
Hottentot Teal <i>Anas hottentota</i>					▲	
Hardhead <i>Aythya australis</i>		▲				
Madagascar Pochard <i>Aythya innotata</i>						□
'Réunion Pochard' <i>Aythya</i> sp.						□
New Zealand Scaup <i>Aythya novaeseelandiae</i>	▲					
Auckland Islands Merganser <i>Mergus australis</i>	□					

TABLE 2

Wildfowl tribes represented in western Indian Ocean, Australasia, South America and Africa.

* Johnsgard (1978) placed Blue Duck *Hymenolaimus malacorhynchos* in Anatini.

Tribe (from Johnsgard 1978)	Tribe in west Indian Ocean (this study)	Tribe in Africa (Brown <i>et al.</i> 1982)	Tribe in Andamans, Sundas, Moluccas and Philippines (this study)	Tribe in Australasia (this study)	Tribe in South America (Blake 1977)
Anseranatini (Magpie Goose)				✓	
Dendrocygnini (Whistling-ducks)	✓	✓	✓	✓	✓
Anserini (Swans and True Geese)				✓	✓
Cereopsini (Cape Barren Goose)				✓	
Stictonettini (Freckled Duck)				✓	
Tadornini (Shelducks and Sheldgeese)	✓	✓	✓	✓	✓
Tachyerini (Steamer Ducks)					✓
Cairinini (Perching Ducks)	✓	✓	✓	✓	✓
Merganettini (Blue and Torrent Duck)*				✓	✓
Anatini (River Ducks)	✓	✓	✓	✓	✓
Aythiini (Pochards)	✓	✓		✓	✓
Mergini (Sea Ducks)				✓	✓
Oxyurini (Stiff-tailed Ducks)	✓	✓		✓	✓

Zealand) have also proven difficult to place (see Callaghan 2005b). These very distinctive ducks generally now comprise their own tribe (Malacorhynchini), an early branch of the true ducks (subfamily Anatinae); however, this placement is very tentative, as, possibly, is the inferred relationship between the two genera.

There are also representatives in the region of larger 'modern' wildfowl tribes that have no extant relatives in adjacent continental areas (e.g. *Cygnus*, *Mergus* and *Oxyura*). The absence of these genera from the nearby mainland further suggests early radiations in the region during previous geological periods, when wildfowl habitats may have been different. As a consequence of sea level rises following the Pleistocene, a diverse range of taxa from both ancient and modern wildfowl groups has evolved on islands.

Taxonomic revisions have frequently changed the status of island forms. The Madagascan Meller's Duck *Anas melleri*, once considered a poorly differentiated island isolate of the Holarctic Northern Mallard *A. platyrhynchos* is currently deemed a much older species with close affinities to African ducks (Young & Rhymer 1998). The extinct Amsterdam Island Duck *A. marecula* (see below) was initially thought derived from the highly dispersive Palearctic Garganey *A. querquedula* (Bourne *et al.* 1983, Martinez 1987), until closer examination suggested that the species was a form of wigeon (Olson & Jouventin 1996).

Resident populations of the widespread whistling-ducks *Dendrocygna viduata* and *D. bicolor* have become established in Madagascar and are undifferentiated from those elsewhere in the world. The presence of so many whistling-duck taxa in the region (six of eight species of *Dendrocygna* and the single species of *Thalassornis*; three of them endemic species) is interesting, although its significance in the evolution of this subfamily is unclear (Livezey 1995). There is also a high number of species of Tadornini (shelducks and sheldgeese) in the region. The limits of this group are contentious, however, as the five genera recognised by Callaghan & Harshman (2005; including three recently extinct *Alopochen* species from the Malagasy Region) and the poorly known subfossil genera *Centronis* (Madagascar: Livezey 1997, Goodman & Hawkins 2003) and *Pachyanas* (New Zealand: Worthy & Holdaway 2002) include 20 species, of which nine occur in the region compared with six in South America and four in Africa.

The African origin of many wildfowl in Madagascar is unsurprising and three Afrotropical species (*Anas erythrorhynchos*, *A. hottentota* and *Nettapus auritus*) and *Sarkidiornis melanotos* (found in the Afrotropical and Oriental Regions, with a sister species, *S. sylvicola*, in South America) are widespread and resident throughout Madagascar. Migration between Madagascar and mainland Africa has never been observed, but has been proposed for at least one species (*A. erythrorhynchos*: Langrand 1990). The endemic Madagascar White-backed Duck *Thalassornis leuconotus insularis* is a small, dark, form of this Afrotropical species (Young 2005) and the endemic Meller's Duck, undoubtedly a long-established species in Madagascar, appears to have shared-ancestry with two African species, Black Duck *A. sparsa* and Yellow-billed Duck *A. undulata* (Young & Rhymer 1998). Four extinct

sheldgeese are known from the Malagasy Region (*Centrornis majori* and *Alopochen sirabensis* in Madagascar; *A. mauritanus* in Mauritius; and *A. kervazoi* in Réunion), and those placed to date in *Alopochen* are presumably closely related to African *A. aegyptiacus* (Livezey 1997).

Surprisingly, with many islands in the region lying close to the Asian mainland, only a small number of continental species (Radjah Shelduck *Tadorna radjah*, White-winged Duck *Asacornis scutulata* and Cotton Teal *Nettapus coromandelianus*) have forms in the region, and there is also only one, undifferentiated, wildfowl species (Lesser Whistling-duck *D. javanica*) resident. Mallards are represented in the Philippines by Philippine Duck *Anas luzonica* and in Australasia by Pacific Black (Grey) Duck *A. superciliosa* which are, with the mainland's spot-billed ducks *A. poecilorhyncha* and *A. zonorhyncha*, members of an Asian subgroup within the mallard clade (Livezey 1997, Johnson & Sorenson 1999). The Australian pochard, Hardhead *Aythya australis*, is a member of an *Aythya* clade (the white-eyed pochards) with the Ferruginous Duck *A. nyroca* and Baer's Pochard *A. baeri* representing Asian populations, whilst New Zealand's scaup *A. novaeseelandiae* is a member of an entirely different pochard clade (the scaup), which includes Greater Scaup *A. marila*, Lesser Scaup *A. americana* and Tufted Duck *A. fuligula*. The two Australasian pochards, Hardhead and New Zealand Scaup, have quite distinct origins (Livezey 1997). Madagascar Pochard *A. innotata* (see below) is another white-eyed pochard that may be more closely related to the Australian species. Subfossil remains of an *Aythya* in Réunion have been tentatively linked to *A. innotata* but may be a distinct taxon (Mourer-Chauviré *et al.* 1999).

Blue-billed Duck *Oxyura australis* is part of a recent clade within the stifftail tribe (Oxyurini), which includes Afrotropical *O. maccoa* and Palearctic *O. leucocephala* (McCracken & Sorenson 2004) (note, the extinct New Zealand population of *O. australis* (see Horn 1983) is now considered a misidentification: Holdaway *et al.* 2001).

Palearctic affinities in the region's wildfowl are most obvious on the subantarctic islands but representatives of several genera such as swans (*Cygnus*), pochards (*Aythya*), stifftails (*Oxyura*) and mergansers (*Mergus*) today have closest relatives in the Palearctic. The southern taxa, at the same time as their current northern counterparts, may have evolved following isolation in the Southern Hemisphere. The number of swan species in the region has been debated. Black Swan *C. atratus* is common in Australia and New Zealand, and migrants have repopulated areas where they were exterminated by Polynesian settlers (Holdaway *et al.* 2001, Williams 2003). Further introductions have occurred following the arrival of Europeans. New Zealand's extinct swan population was originally described, from subfossil remains, as *C. sumnerensis* (Livezey 1989, Turbott 1990), but separation from *C. atratus* is no longer accepted (Worthy & Holdaway 2002). Another extinct swan, which once occurred on the Chatham Islands, is awaiting analysis and may be distinct from the Black Swan (Holdaway *et al.* 2001).

The ducks of the remote subantarctic islands owe their origins to a variety of source species. The pintail taxa, Eaton's Pintail *Anas eatoni*, resident on Kerguelen (*A. eatoni eatoni*) and Crozet (*A. eatoni drygalskii*) are considered to be forms of the Holarctic Northern Pintail *A. acuta* (Marchant & Higgins 1990). The extinct flightless ducks of Amsterdam and St Paul (*A. marecula* and an undescribed taxon, respectively) are probably forms of wigeon (three species of wigeon occur outside the region). Interestingly, whilst the undescribed (and potentially flightless) duck from St Paul may be related to and share a common ancestor with *A. marecula*, it is also possible that it represents a different taxon (Olson & Jouventin 1996).

Brown teals are known from New Zealand (*A. chlorotis*) and three isolated subantarctic island groups: the Aucklands (*A. aucklandica*), Campbells (*A. nesiotis*) and Macquarie (undescribed taxon, see Holdaway *et al.* 2001), all of which islands are included within New Zealand for the purposes of this publication. *A. aucklandica* and *A. nesiotis* are flightless (flightlessness is indeterminate in the Macquarie species, but would be expected). This radiation is separate from the similar diversification within the related grey teal (see below), and the ancestral brown teal most likely reached New Zealand well before the modern radiation of grey teal (Daugherty *et al.* 1999, Kennedy & Spencer 2000).

Dispersal of taxa within the region

There is significant evidence to show that some wildfowl have dispersed within the region, without obvious additional contact with continental areas. Grey teal taxa are resident in Australia (Chestnut Teal *A. castanea*), Australia, New Zealand, New Guinea and New Caledonia (Grey Teal *A. gracilis*), the Sundas and Moluccas (Indonesian Teal *A. gibberifrons*), Andamans (Andaman Teal *A. albogularis*) and Madagascar (Madagascar Teal *A. bernieri*). Populations of grey teal are still often highly dispersive. As these species are adapted to saline waters and breed in mangrove habitat, a possible pattern of dispersal by a common ancestor during Pleistocene sea level changes is postulated (Young 2002), particularly as lower sea levels would have permitted the development of extensive mangroves. The extinct duck from the Mascarenes, Sauzier's Teal *A. theodori* was probably also a grey teal (Mourer-Chauviré *et al.* 1999) and other taxa in this clade may have been resident in areas now submerged.

The wildfowl fauna of New Zealand provides further evidence of movement within the region, revealing an obvious connection with Australia; many forms have presumably colonised directly from the larger island. Of 18 recent species (Table 1), four (*Cygnus atratus*, *Anas superciliosa*, *A. gracilis* and *A. rhynchotis*) have populations in both islands and a further seven (*Cnemiornis* (two species, with *Cereopsis*), *Tadorna* (two species including the undescribed Chatham Island Shelduck), *Chenonetta* (*Eurynas*), *Malacorhynchus* and *Biziura* have counterparts in Australia. The four brown teals probably also evolved from a common ancestor of this group and the grey teal that reached New Zealand from Australia.

The fall

The decline of the region's wildfowl during recent times follows an all-too predictable course and one that has been thoroughly documented elsewhere (see e.g. Olson & James 1984, Milberg & Tyrberg 1993, Steadman & Martin 2003). Typically, the discovery and subsequent colonisation of the more remote islands by humans heralded the decline of their wildfowl faunas. The exact agents of extinction on specific islands are sometimes debatable but habitat modification, predation from and competition with exotic animals and direct persecution, are all generally anthropogenic in source.

In New Zealand, 18 species of wildfowl were resident at first human contact (Holdaway *et al.* 2001). Not included in this number is *Anas rhynchos*, as this species is considered to have immigrated naturally since human colonisation c.1,000–1,200 years ago (Cassels 1984). The first Polynesian settlers colonised New Zealand around 800 years ago and they and their commensal mammals initiated a cycle of faunal extinctions throughout the archipelago that has resulted in nine wildfowl species (50%) becoming extinct (see Worthy & Holdaway 2002 for details of the decline of New Zealand's fauna and list of references).

The Chatham Islands (New Zealand) were first colonised by Polynesians from New Zealand c.400–450 years ago (Tennyson & Millener 1994) and extinctions of wildfowl populations may have occurred later than on the main New Zealand islands. Two species, however, disappeared following the arrival of Europeans, the merganser (see below) and, presumably, the endemic teal of Macquarie. Macquarie was not discovered until 1810, after which it became a base for visiting sealers (Taylor 1979) who presumably exterminated this small insular duck. It was probably also the activities of sealers and commensal mammals that exterminated the Amsterdam and St Paul ducks (possibly as late as 1877), following their discovery and occupation by sealers from the end of the 17th century (Bourne *et al.* 1983, Jouventin 1994).

Similarly, in the western Indian Ocean, extirpation of all native wildfowl in the Mascarenes followed human colonisation early in the 17th century, and all species were extinct by the end of the same century (Cheke 1987). In Madagascar, however, the extinction date of the sheldgeese is unclear. Madagascar has recently undergone a reduction in annual rainfall, being distinctly wetter even just 1,000 years ago (Hawkins & Goodman 2003). Both *Centornis majori* and *Alopochen sirabensis* were once common in the south-west and the central highlands (Young *et al.* 2003), thus aridification, coupled with human agencies following colonisation, may have resulted in the extinction of the sheldgeese.

Two recently extinct species are detailed below.

Madagascar Pochard *Aythya innotata*

The Madagascar Pochard (or Madagascar White-eye) superficially resembles the Palearctic Ferruginous Duck (or Eurasian White-eye), a species that winters in part in Africa and has been recorded in Seychelles (Skerrett 1999). Analysis of

morphological (Livezey 1996) and genetic (Sorenson & Fleischer 1996) material has revealed that the Madagascan species, whilst nestling within a distinct clade of *Aythya* that includes *A. nyroca*, is possibly most closely related to the Australian endemic Hardhead (or Australasian White-eye).

A. innotata was described from Lake Alaotra, an extensive shallow wetland on the Central Plateau (c.1,200 m above sea level) in 1894 (Salvadori 1894), and appears to have been restricted to this site, at least since its discovery. Supposed sightings away from Lake Alaotra (e.g. at Lake Ambohibao, near Antananarivo; Salvan 1970) are doubtful or at least must have represented rare dispersal. Subfossil remains of an *Aythya* are available from Réunion (Mourer-Chauviré *et al.* 1999, Hawkins & Goodman 2003) and these may represent dispersal events or the presence on this island of another, closely related species.

The open water of Alaotra may have always been little used by pochards, as they were probably inhabitants of quiet, well-vegetated pools much like *A. nyroca* (Callaghan & Green 2005). Large areas of the Alaotra basin were once occupied by papyrus and *Phragmites* marsh, most notably in the south. This marsh, though much reduced today, is still typified by numerous quiet pools and abundant emergent vegetation including water lilies *Nymphaea* sp. The wetland also once held another endemic waterbird, the presumably extinct Alaotra (or Delacour's) Grebe *Tachybaptus rufolavatus* and still hosts a population of marsh-living lemurs (*Haplolemur griseus alaotrensis*) that feed exclusively on marsh vegetation.

Examination of the lake system at Alaotra today shows the area to be much reduced from its former extent and, whilst this reduction has been mostly undocumented, it must be assumed that the reduction is largely anthropogenic in origin. The majority of surrounding hillsides have been entirely deforested and resultant siltation has considerably reduced water depth and aquatic biodiversity. Humans first constructed settlements in Madagascar c.1,200 years ago (Dewar 2003) and habitat modification throughout the island has subsequently been extensive. The pochard was described as common at Alaotra in 1929 (Delacour 1954) and 1935 (Webb 1936), and was still present in 1960 (Dee 1986), when the last known sightings were made at the lake. Although described as common in 1978 (Soothill & Whitehead 1978), the species had not in fact been found during several surveys at the lake since 1971 (Dee 1986, Young & Smith 1989, Wilmé 1994). Salvan (1970) provided the last published sighting anywhere, in 1970, away from Alaotra.

Surprisingly, following a publicity campaign amongst villages surrounding Alaotra in 1989, a male was captured by fishermen and taken into captivity in 1991 (Wilmé 1993). Following this, further extensive surveys of Alaotra and adjacent wetlands on the Central Plateau failed to locate more birds (Pidgeon 1996). The captured bird, which died in 1992, is the last known and only photographed individual, and *A. innotata* is now considered extinct.

The rapid decline of *A. innotata* went almost unnoticed, making it now difficult to determine the precise causes. All wetlands in Madagascar have undergone severe anthropogenic modification (Young 1996). These changes, however, probably

commenced subsequent to a lengthy period of natural aridification in parts of the island such as the south-west (Goodman & Rakotozafy 1997). The primary factor attributed to the extinction of the pochard is the introduction into Lake Alaotra (and many other wetlands) of exotic fish. The release of herbivorous cichlids into the lake (e.g. *Oreochromis mossambicus*, *O. niloticus*, *O. macrochir*, *Tilapia rendalli* and *T. melanopleura* in 1955–60; Pigeon 1996) has had considerable affect on the aquatic flora and entire lake system. The subsequent introduction of alien carnivorous species, Black Bass *Micropterus salmoides* and Asian Snakehead *Ophicephalus striatus*, in 1961 and around 1980, respectively (Pigeon 1996), undoubtedly proved detrimental to the lake's waterbirds through both competition and direct predation (the introduction of *M. salmoides* into Lake Atitlán in Guatemala in 1960 has been directly linked to the decline and extinction of the grebe *Podilymbus gigas* endemic to this single lake: BirdLife International 2000). Increasing use by fishermen of monofilament gill nets that catch all unsuspecting diving birds, and pesticide run-off from adjacent rice fields, have placed additional pressures on the lake's waterbirds and probably also caused the extinction of the Alaotra Grebe (Pigeon 1996, Young 1996, Hawkins *et al.* 2000), and may prevent any recolonisation by pochards, or grebes, if an unknown population exists elsewhere in Madagascar.

Auckland Islands Merganser *Mergus australis*

The presence of a merganser in New Zealand and its outlying islands is something of a biogeographic enigma, as is the bird's phylogenetic relationships. Only two Mergini have been identified as having Holocene distributions in the Southern Hemisphere but, according to Livezey (1989b), Auckland Islands Merganser *Mergus australis* and Brazilian Merganser *M. octosetaceus* are not close relatives; the former representing an early and unique branch in the merganser clade, the latter being closely related to Northern Hemisphere *M. serrator* and *M. squamatus*.

At the time of first human contact, *c.*800 years ago, *M. australis* was apparently distributed around the coasts of New Zealand's three main islands (North, South and Stewart), was a member of the extensive waterfowl fauna in the Chatham archipelago (650 km east of New Zealand), and occurred on the subantarctic Auckland Islands (400 km south of New Zealand) (Millener 1999, Worthy & Holdaway 2002). McCormick's (1842) claim of their presence on subantarctic Campbell (600 km south of New Zealand) is considered a misidentification. *Mergus* bones have been found in numerous coastal fossil deposits, particularly at the heads of large and sheltered bays, from the north-eastern tip of North Island to Stewart Island, and in middens at some river mouths and estuaries in all three main islands (Worthy & Holdaway 2002). On Chatham, *Mergus* bones are common in fossil and midden deposits especially fringing the extensive saline Te Whanga Lagoon (Millener 1999). Within the Auckland group, subfossil bones have been found at the heads of some sheltered eastern inlets (Kear & Scarlett 1970).

The Chatham Islands, which prior to sea level rises at the end of the Pleistocene was a large and extensive archipelago, had a rich avifauna of at least 100 species

(Millener 1996, 1999) and many species, clearly of New Zealand origin, have differentiated and are recognised as unique taxa (Turbott 1990). Millener (1999) considered the Chatham population of *Mergus* to represent an undescribed species, being smaller than the Aucklands population, with a shorter bill and reduced wings. This distinction, however, was not supported by Worthy & Holdaway (2002), who pointed to the considerable size variation evident in Chatham and mainland New Zealand populations.

The early Polynesian settlers of New Zealand significantly altered the faunal composition of the islands, producing what has become among the best documented of recent human-induced extinction events (Worthy & Holdaway 2002). *Mergus* was one of eight waterfowl species exterminated within, perhaps, 300 years of the settlement of New Zealand, and amongst six waterfowl species subsequently exterminated on the Chathams when this archipelago too was settled (Millener 1999).

Historic accounts of Auckland Islands Merganser are restricted to its distribution within the Auckland group (Kear & Scarlett 1970). The first specimen to be collected for science was in 1840, in Laurie Harbour, a northern inlet, but all subsequent sightings appear to have been made within the confines of the southern Carnley Harbour. The assiduous collector, W.L. Buller (1891) commented 'It is very desirable that specimens of this interesting form in the adult state should be obtained for our museums before it is too late', further pointing out that 'Although ...(during) periodical visits to Auckland Islands...eager search is made, the bird is scarcely ever seen'. Thus, the Auckland Islands Merganser was sought-after by subsequent visitors, along with another endemic waterfowl, the flightless Auckland Island Teal *Anas aucklandica*. Kear & Scarlett (1970) reported the whereabouts of 26 specimens, 20 of which were collected post-Buller's 1891 remarks and the last two were apparently shot on 9 January 1902. As seven specimens were reputedly taken in 1901 alone (Kear & Scarlett 1970), the possibility exists that collecting was the ultimate cause of its extinction.

Few reports were made on the ecology of this species. No nest was ever recorded and there is only one written observation of the young (a brood of four, which were collected; Chapman 1891). Confusion also surrounds its primary habitat—was it a sea duck or mostly an estuarine and freshwater inhabitant? Kear & Scarlett (1970) collated all known references and reported a rare observation of birds in a small, steep-flowing stream. However, all other observations in Carnley Harbour appear to have been at the heads of sheltered bays near the emergence of freshwater streams. ^{15}N and ^{13}C isotope signatures of two fossil bones from separate New Zealand sites suggest both freshwater and marine foods (R. Holdaway, M. Williams unpubl. data).

The other islands

Interestingly, whilst the fall of the Anseriformes in the western Indian Ocean, New Zealand and subantarctic islands has been dramatic, the other island groups in the region have seen no recent wildfowl extinctions. In Australia, megafaunal collapse following the arrival of humans c.50,000 years ago is well documented (Miller *et al.*

TABLE 3

Status of resident wildfowl taxa in island groups of the western Indian Ocean and Australasia. Madagascar includes islands of the Malagasy Faunal Region (see Table 1), Subantarctic Islands includes Amsterdam, Crozet, Kerguelen and St Paul.

IUCN status is from TWSG (2004) and includes Critical, Endangered and Vulnerable.

Island group	No. of recent taxa (see Table 1)	No. of extinct taxa (see Table 1)	No. of endangered taxa IUCN status (TWSG 2003)
New Zealand	18	9	4
Australia	19		
New Guinea	9		1
Philippines	3		1
Sundas	5		1
Moluccas	4		
Andaman Islands	2		1
Madagascar	16	7	3
Subantarctic islands	4	2	2

2005) and extinctions include a possible Anseriform (*Dromornis* sp.; Vickers-Rich & Rich 1999). This may be due to the adaptation of wildfowl to human presence on islands closer to mainland areas, or that the remains of fossil taxa have yet to be discovered. The current status of the remaining taxa in the region, however, should not give rise to complacency—of 38 endemic species, 13 (34%) are listed by IUCN as Critical, Endangered or Vulnerable (TWSG 2003; Table 3).

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Recent avian extinctions on Réunion (Mascarene Islands) from paleontological and historical sources

by Cécile Mourer-Chauviré, Roger Bour & Sonia Ribes

The Mascarene Islands were uninhabited when the first Europeans settled there, during the 16th century. The strange avifauna of these islands was described by the early travellers, but many species disappeared very rapidly. Fossil remains were discovered very early on Rodrigues, and later on Mauritius, but it was only in 1974 that the first remains of fossil birds were discovered on Réunion, in a large cave, 'Grotte des Premiers Français'. Subsequently, other remains were discovered in small basaltic caves and in a marsh. These fossil birds were studied by Cowles (1987, 1994), Mourer-Chauviré & Moutou (1987), Mourer-Chauviré *et al.* (1994, 1995a,b), following which a comprehensive paper concerning the different species and fossiliferous localities was issued (Mourer-Chauviré *et al.* 1999).

The original avifauna of Réunion is also known from the accounts of early visitors, whose reports were collated by Lounnon (1970). The parts concerning birds are also presented by Barré & Barau (1982) and Barré *et al.* (1996). Particular parts of these accounts were discussed by Cheke (1987), and a previously unknown report, by Melet, who called at Réunion in 1671, was discovered by Anne Sauvaget and published in 1999 (Sauvaget 1999).

The solitaire

Several early travellers mentioned a large, almost flightless, whitish bird called the solitaire which, following the discovery of 17th-century paintings, was generally admitted to be a white dodo. However, in 1980 the remains of a large, extinct insular ibis, initially named *Borbonibis latipes* (Mourer-Chauviré & Moutou 1987), were discovered. It was some surprise that this bird had never been mentioned in the early reports. As further remains of the ibis were found in other localities in the west of the island, it must have been relatively abundant in areas near the coast, i.e. where the first navigators landed. During our excavations, and despite our expectations, we never found a fossil bone attributable to a dodo. Re-analysis of the early accounts led us to the conclusion that the Réunion solitaire was not a dodo but the above-mentioned ibis. In terms of its osteological characteristics, the ibis is related both to *Threskiornis aethiopicus*, Sacred Ibis, and *T. spinicollis*, Straw-necked Ibis.

The descriptions of the solitaire, given by the travellers, agree well with an ibis and some cannot apply to a dodo. Abbé Carré, who was on Réunion in 1667, stated: 'It would look like a turkey, if it did not have higher legs. The beauty of its plumage is a delight to see. It is of changeable colour which verges upon yellow'. Melet, who visited Réunion in 1671, wrote: 'and other kinds of birds that are called Solitaires, which are very tasty, and the beauty of their plumage is very curious by the diversity

of bright colours which shone on their wings and around their neck'. Sieur Dubois, who was present on Réunion in 1671–72, elaborated: 'These birds are so-called (Solitaires) because they always go alone. They are as big as a large goose and have white plumage, black at the tip of the wings and tail. At the tail there are feathers approaching those of the ostrich. They have a long neck and the beak made like that of the woodcock, but bigger, and legs and feet like the turkeys. This bird is caught by running after it, since it flies only very little'. Feuilley, visiting Réunion in 1704, added: 'The Solitaires are the size of an average turkey cock, grey and white in colour. They inhabit the tops of the mountains. Their food is only worms and filth, taken on or in the soil' (after Barré & Barau 1982, Sauvaget 1999, our translation). The long legs, black wingtips and tail, long neck, beak like that of a woodcock but stronger and food consisting of worms taken on or in the soil do not correspond to a dodo, which had a strong, inflated bill and was frugivorous. The bright colours on the wings and neck are reminiscent of the iridescent plumage of Straw-necked Ibis. Sieur Dubois is the only author to mention that the solitaire was still able to fly.

The only accounts *contra* this interpretation are those of Tatton and Bontekoe. Tatton, who was on Réunion in 1613, wrote: 'A great fowl, the bigness of a Turkie, very fat and so short-winged that they cannot flie, being white, and in a manner tame', single and Bontekoe, who called in at Réunion in 1619, suggested: 'There were also some Dod-eersen, which had small wings but could not fly; they were so fat that they could scarcely walk, for when they walked their belly dragged along the ground' (Fuller 2002). But Bontekoe's ship was blown up and his account was published only in 1646. It is likely that 'having a recollection of a large brevipennate bird in Bourbon, whose tameness rendered it an easy prey to his sailors, he concluded it to be a Dodo, and adopted the name and descriptions of that bird which had been given by previous navigators' (Strickland & Melville 1848). For their part, Hume & Cheke (2004) have demonstrated that all of the paintings of white dodos were based on an early picture, by Roelant Savery, of a whitish specimen of a Mauritius Dodo *Raphus cucullatus*, painted in Prague c.1611.

Another objection to the occurrence of a true dodo on Réunion is the island's very recent geological age. Recent work on the DNA of Mauritius Dodo and Rodrigues Solitaire *Pezophaps solitaria* have revealed these two to be sister taxa and that their closest living relative is Nicobar Pigeon *Caloenas nicobarica*. The maximum likelihood molecular clock indicates 'that the dodo/solitaire and *Caloenas* diverged in the mid/late Eocene, around 42.6 million years ago (Ma) (95% confidence interval = 31.9 to 56.1 Ma), whereas the dodo and the solitaire separated in the late Oligocene, about 25.6 Ma (17.6 to 35.9 Ma)' (Shapiro *et al.* 2002). These analyses suggest that the lineages of the dodo and Rodrigues Solitaire diverged a very long time ago. The age of Mauritius and Rodrigues is estimated at 8–10 Ma (Hume & Cheke 2004), whilst Réunion only dates 3 Ma (Molnar & Stock 1987). Much of the Réunion fauna and flora derives from Mauritius and it is probable that, when Réunion emerged from the sea, the ancestors of the dodo and Rodrigues

Solitaire had already lost their ability to fly, and were thus no longer able to colonise the newly appeared island (Hume & Cheke 2004).

In conclusion we consider that, for now, there is no paleontological or pictorial evidence for the existence of a white dodo on Réunion, and that the descriptions of the solitaire agree better with the extinct ibis which has been found in several localities and is now named *Threskiornis solitarius* (Séllys-Longchamps, 1848) (Mourer-Chauviré et al. 1995b).

Other species, extinct or extirpated from Réunion, described by the navigators and found as fossils

***Nycticorax duboisi* (Rothschild, 1907), Réunion Night Heron**

The description given by Dubois is: 'Bitterns or Great gulleets, large as big capons (*Gallus gallus*) but fat and good (to eat). They have grey plumage, each feather tipped with white, the neck and beak like a heron and the feet green, like the feet of the 'Poulets d'Inde' (*Meleagris gallopavo*). That lives on fish' (Barré & Barau 1982, our translation). Two probably flightless species of night herons also formerly occurred in the Mascarenes, on Mauritius (*Nycticorax mauritianus*) and Rodrigues (*N. megacephalus*). Unlike these two forms, the proportions of the wing and leg bones of the Réunion heron show that it had flight capabilities quite similar to that of living species.

***Phoenicopterus ruber* Linnaeus, 1758, Greater Flamingo**

Greater Flamingos were mentioned several times in historical accounts of Réunion (Lounnon 1970) and Feuilley indicated that there were 3,000–4,000 of them in 1704 on the Etang du Gol (Barré & Barau 1982). They disappeared between 1710 and 1730 (Cheke 1987).

***Alopochen (Mascarenachen) kervazoi* (Cowles, 1994), Kervazo's Egyptian Goose**

Several reports mention the presence of geese, but only until the time of Dubois, who gave the most detailed description: 'wild geese, slightly smaller than the European geese. They have the same feathering, but with the bill and feet red. They are very good [to eat]' (Barré & Barau 1982, our translation). The identification of this goose as closely related to *Alopochen aegyptiacus*, Egyptian Goose, agrees well with Dubois' description of the red bill and the feet. The extinct goose of Réunion, and the extinct Malagasy Goose *Alopochen sirabensis*, exhibit a slight reduction in the length of the wing elements (ulna and carpometacarpus), and a slight increase in the length of the femur.

***Anas theodori* Newton & Gadow, 1893, Sauzier's Teal, and cf. *Aythya* sp., a Pochard**
Dubois mentions: 'River ducks, smaller than European ones, feathered like teals. They are good [to eat]' (Barré & Barau 1982, our translation). The *Anas* remains

from Réunion are attributed to the same species as that described from Mauritius. The dimensions of the bones do not indicate a diminished flying ability. It is thus possible that the species could fly between Mauritius and Réunion.

***Falco duboisi* Cowles, 1994, Réunion Kestrel**

Dubois and another author mentioned kestrels. Dubois noted three different birds of prey. The first were Réunion Harriers *Circus maillardi*, a still-extant species. 'The second ones are named yellow-feet, with the size and shape of falcons' (Barré & Barau 1982, our translation). The Réunion Kestrel is much larger than the endemic insular kestrels *Falco araea* (Seychelles Kestrel) and *F. newtoni* (Madagascar Kestrel), and slightly larger than *F. punctatus* (Mauritius Kestrel). It also differs from the latter by its less-reduced wings.

***Dryolimnas augusti* Mourer-Chauviré et al., 1999, Réunion Wood Rail**

Dubois was the only author to mention rails, and he simply wrote that there were wood rails. The rail remains have been attributed to the genus *Dryolimnas* and they differ from the recent species, *D. cuvieri*, White-throated Rail, in their larger size and by the shape of the tarsometatarsus which is much more robust. The proportions of the wing elements compared to those of the leg reveal that the Réunion Wood Rail was flightless, a characteristic of the extant subspecies *D. cuvieri aldabranus*, of Aldabra, whilst the nominate taxon from Madagascar remains volant.

***Fulica newtonii* Milne-Edwards, 1867, Newton Coot**

A large, extinct species of coot was described by Milne-Edwards from remains found at the Mare aux Songes, Mauritius. The remains found on Réunion do not differ. This form is related to extant *Fulica cristata*, Red-knobbed Coot, which is principally found in Africa and Madagascar, but is slightly larger. The proportions of the bones indicate some reduction in flying ability. Many authors have reported the presence of water hens, but the most detailed description is given by Dubois: 'Water hens, which are as big as hens. They are completely black and have a big white crest on the head' (Barré & Barau 1982, our translation).

***Nesoenas duboisi* Rothschild, 1907, Réunion Pink Pigeon**

All the early navigators, including Feuilleux in 1704, noted the abundance of pigeons and doves. Despite this, we have found only two remains attributable to this pigeon. They differ from the genus *Alectroenas*, being more similar to Mauritius Pink Pigeon *Nesoenas mayeri*, and correspond to the description given by Dubois of russet-red wild pigeons: 'They are a little larger than the European Pigeons, and have a stronger bill, red at the end close to the head, the eyes ringed by flame colour, like the pheasants' (Barré & Barau 1982, our translation). A molecular study of the genera *Streptopelia* and *Columba* has shown Mauritius Pink Pigeon to be sister to *Streptopelia picturata*, Madagascan Turtle Dove (Johnson et al. 2001). These authors suggested the genus *Nesoenas* be merged with *Streptopelia*, but Cheke

(2005) emphasised the similarities between *picturata* and *mayeri* and their differences compared to other *Streptopelia*, and proposed retention of *Nesoenas* which should also include *picturata* (the position adopted here).

***Mascarinus mascarinus* (Linnaeus, 1771), Mascarene Parrot**

The early travellers also spoke of the very large quantity and diversity of parrots, of which at least four species occurred on Réunion. We have found few remains attributable to the Mascarene Parrot. Dubois' description, 'Parrots a little bigger than pigeons, the feathering of the colour of petit-gris, a black hood on the head, the beak very strong and the colour of fire' (Barré & Barau 1982, our translation), agrees very well with *Mascarinus mascarinus* which is known from late-18th-century illustrations. Petit-gris is the name given to the fur of Eurasian Red Squirrel *Sciurus vulgaris* in its dark phase.

***Fregilupus varius* (Boddaert, 1783), Réunion Starling**

We have found one bone of Réunion Starling. The description given by Dubois agrees well with this species which is known from 18th-century illustrations and specimens: 'Hoopoes or 'Callendres', with a white tuft above the head, the rest of the plumage white and grey, the beak long, and the feet as that of a bird of prey' (Barré & Barau 1982, our translation).

Species mentioned historically for which fossils and specimens are unavailable

***Cyanornis* (?=*Porphyrio*) *caerulescens* (Sélys-Longchamps, 1848), Oiseau bleu**

The presence of a large, blue bird was first mentioned by Dubois, without indication of locality, but all subsequent writers reported that it was found in the plains above the mountains and mainly at 'Plaine des Cafres', in the south-west part of the island, more than 1,500 m above sea level. As yet, no fossil remains have been found, which is probably attributable to its distribution; it was not present in that part of the island where all the fossiliferous localities are located.

Dubois wrote: 'Oiseaux bleus, as big as solitaires. Their plumage is all blue, their bill and feet red, made as the feet of fowls. They do not fly but they run extremely fast, so that a dog has difficulty to catching them when hunting. They are very good [to eat]' (Barré & Barau 1982, our translation). According to a report attributed to a certain Father Brown (see Cheke 1987): 'It rarely flies, always hugging the ground, but it runs with surprising speed' (Olson 1977). Taking into account its size and that it was not entirely flightless, Olson (1977) and Cheke (1987) considered it possible that this bird belonged to the genus *Porphyrio*.

Extinct species not reported by the early travellers

Mascarenotus grucheti Mourer-Chauviré et al., 1994, Gruchet's Lizard Owl

We found, in several localities, the remains of a Strigid owl never reported in the historical accounts. We referred it to a new genus, *Mascarenotus*, which includes the three Mascarene owls, *M. murivorus* (Milne-Edwards, 1873), of Rodrigues, *M. sauzieri* (Newton & Gadow, 1893), of Mauritius, and *M. grucheti*, of Réunion. The last two have a much-elongated tarsometatarsus, a characteristic of other, extant insular species, e.g. *Gymnoglaux lawrencii*, Cuban Screech-owl, *Otus nudipes*, Puerto Rican Screech-owl, and in the extinct insular species of the genus *Grallistrix*, from Hawaii (Olson & James 1991). The tarsometatarsi of *M. grucheti* were almost the same size as those of *M. sauzieri*, whilst the wing bones, of which only an incomplete humerus is available, were slightly smaller than that of *M. sauzieri*. However, two left ulnae have recently been found in a new locality, the Caverne Payet, at Grande Chaloupe, on the north coast of the island. These confirm that in Gruchet's Lizard Owl the wings were more reduced than in the other Mascarene owls (Fig. 1, Table 1).



Figure 1. Two left ulnae of *Mascarenotus grucheti* from Caverne Payet, Grande Chaloupe, Réunion (B and C), Muséum d'Histoire naturelle de La Réunion, nos. MHN-RUN-CP-O 1966–67, compared with an ulna of *Mascarenotus sauzieri*, from Montagne du Pouce, Mauritius (A), Muséum national d'Histoire naturelle, Paris, no. MAD 7192. Natural size.

TABLE 1

Measurements of the humeri and ulnae of the three species of *Mascarenotus*.

(1) material from Mare aux Songes and Montagne du Pouce (Thirioux collection), Mauritius, Muséum national d'Histoire naturelle, Paris. (2) after Günther & Newton 1879. (3) humerus from Grotte des Premiers Français, no. LAC 1993-50, MNHN Paris, and ulnae from Caverne Payet, nos. MHN-RUN-CP-O 1966-67, Muséum d'Histoire naturelle de La Réunion.

Humerus	Ulna		
<i>M. sauzieri</i> , Mauritius			
Total length (1)	extremes	65.0–71.5	72.0–86.0
	mean (<i>n</i>)	67.10 (5)	79.25 (6)
<i>M. murivorus</i> , Rodrigues			
Total length (2)	extremes	64.0–69.0	-
	mean (<i>n</i>)	67.50 (2)	74.0 (1)
<i>M. grucheti</i> , Réunion			
Total length (3)	extremes	-	64.0–66.4
	mean (<i>n</i>)	est. 60.5 (1)	65.20 (2)

Species extant on Réunion also known from fossils

Puffinus pacificus (Gmelin, 1789), Wedge-tailed Shearwater

Puffinus lherminieri Lesson, 1840, Audubon's Shearwater

Phaethon lepturus Daudin, 1802, White-tailed Tropicbird

Numenius phaeopus (Linnaeus, 1758), Whimbrel

Nesoenas picturata (Temminck, 1813), Madagascar Turtle Dove (Cheke 2005)

Chronology of the extinctions

From the early accounts and the fossil record, at the time when Europeans settled Réunion, the avifauna included at least 33 species of resident landbirds. Of these, 17 are extinct, five no longer occur on Réunion, and 11 are extant there. Amongst the 11 survivors, eight are very small (Apodiformes and Passeriformes) and *Coracina newtoni* (Pollen), Réunion Cuckoo-shrike, is globally threatened.

The historical reports enable us to follow the chronology of extinctions, which occurred very rapidly, over a period of two centuries from 1646. A first group of species, reported by the earliest visitors and by Dubois in 1671–72, apparently became extinct almost immediately because they were not reported thereafter, namely: *Nycticorax duboisi*, *Alopochen* (*M.*) *kervazoi*, *Anas theodori*, a pochard, *Falco duboisi*, possibly a smaller falcon known as Émerillon, *Dryolimnas augusti*, *Fulica newtonii*, a parrot known as 'Perroquet vert à tête... couleur de feu', and a *Foudia* sp. Rats were absent in 1671, as indicated in the log of Le Breton and by Dubois, but had invaded by 1675 (Cheke 1987). The first wave of extinction mainly included aquatic forms inhabiting the ponds and marshes of the west coast, the first area to be settled.

The second wave of losses included species mentioned by Feuilley in 1704 but not recorded thereafter. These included a cormorant, probably *Phalacrocorax africanus* (Long-tailed Cormorant), an egret, probably *Egretta garzetta dimorpha* (Dimorphic Egret), *Phoenicopterus ruber*, *Alectroenas* sp., a blue-pigeon, *Nesoenas duboisi*, and perhaps another dove. The Réunion solitaire *Threskiornis solitarius* survived for a short time, taking refuge in the mountains, but was reported for the last time in 1708. Cats were introduced in 1703 to exterminate rats and must have played a significant role in the destruction of the birds. Thereafter, in 1734–63, Oiseau bleu (Cheke 1987), a grey parrot and a parakeet, *Psittacula eques/echo*, disappeared, followed c.1780 by *Mascarinus mascarinus*, and lastly, in 1838–58, by *Fregilupus varius* (Barré & Barau 1982).

It is well known that Réunion's birds were so tame that a single man, armed with a simple stick, could kill up to 200 of them in one day (see Mourer-Chauviré *et al.* 1999). Man has certainly played a direct role in the extinction of these birds, and that of the giant land tortoise, *Cylindraspis indica* (Austin *et al.* 2002), but has also played an indirect role by introducing predators (pigs, rats, cats) or competitors, and by destroying habitats. Finally, it is also possible that the introduction of a disease or parasite wrought the extinction of the Réunion Starling (Cheke 1987).

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Unpublished drawings of the Dodo *Raphus cucullatus* and notes on Dodo skin relics

by *Julian Pender Hume, Anna Datta & David M. Martill*

The Dodo *Raphus cucullatus* was an endemic giant flightless pigeon from Mauritius that died out within 100 years of its discovery in 1598 (Moree 1998, Hume *et al.* 2004). It has become a metaphor for extinction, exemplifying man's destructive capabilities on endemic oceanic island species (Fuller 2002). Our scant knowledge of the Dodo's morphology and autecology is derived largely from historical accounts, including contemporary paintings and ships' records, although there has been debate as to their scientific accuracy (Kitchener 1993). Knowledge of the skeletal anatomy of the Dodo is more detailed, being derived mainly from fossil remains discovered in the Mare aux Songes in the 1860s (Owen 1866). Very few Dodo remains reached European shores, and thus very few scientists have ever had 'hands-on' experience of this enigmatic bird. Such was the paucity of tangible evidence for the existence of the Dodo that in the early 19th century many considered the species to have been mythical (Strickland & Melville 1848). Here we announce the discovery of 19th-century illustrations of a Dodo foot, executed by John Edward Gray, while searching the archives in the general library of the Natural History Museum, London.

Although a number of exotic species were brought back to Europe in historic times, the inability to keep animals alive, or to preserve dead material on long sea voyages in the 1600s, resulted in comparatively few zoological specimens reaching European shores. Despite suggestions to the contrary (e.g. Hachisuka 1953), as few as four or five Dodo specimens—maybe even fewer—reached Europe, and only one perhaps two birds arrived alive (Hume in press). Amongst the imported birds was the so-called 'Oxford Dodo', a specimen which today comprises the only extant skin remains. It has been suggested that the Oxford example is the same Dodo as that seen alive in London in 1638 (Strickland & Melville 1848), but no substantive evidence to support this claim exists. Further examples of soft tissue dodo specimens once existed in Copenhagen (head) and Prague (beak and foot), but today only the bones are preserved and their histories are uncertain. Furthermore, at least one other specimen of a dodo, if indeed it was actually so, was reported to have been deposited at the Anatomy School, Oxford (e.g. Newton & Gadow 1896), but again, its provenance and subsequent history are unknown.

Brief historical review

The Oxford Dodo has a complex history, having been exhibited as a stuffed bird in the collection of horticulturist John Tradescant (Tradescant 1656), in 1656, and bequeathed to Elias Ashmole in 1659 (Strickland & Melville 1848). The specimen remained in the Ashmolean Museum until its transfer to the Oxford University



Figure 1. Newly discovered unsigned illustrations of the Dodo *Raphus cucullatus* head in dorsal and lateral views, executed by John Edward Gray, c.1824.



Museum during the 1850s. There was a long-held belief that this, by then unique, stuffed Dodo was thrown onto a fire in 1755, and that only the head and a foot were rescued from the flames (e.g. Strickland & Melville 1848, Fuller 2002). In fact, its removal from exhibition was a curatorial decision made to preserve what was left of the by then highly degraded specimen (Ovenell 1992). The salvaged remains included the skin of the head, some feathers and a foot. Today, all that remains of this specimen are two halves of the skin of the head, now with very few feathers, the skull, and the bones of the right foot with some scraps of skin and sinew (Figs. 4–5).

Figure 2. Only known illustration of the ‘Oxford Dodo’ foot alongside the ‘London foot’. The Oxford foot is more gracile and 11% smaller than the latter. They are here interpreted as male (London) and female (Oxford). Annotations in Gray’s hand give dimensions of the feet.



Figure 3. Head prior to dissection, executed by William Clift.



Another Dodo foot termed the 'London foot', which could be seen in a residence formerly called the Music House, situated near the West End of St Paul's church, London, was collected by Hubert alias Forges (Forges 1665). It was presented to the Royal Society of London and transferred to the former British Museum, where it was exhibited along with the most famous Dodo painting (Strickland & Melville 1848), once owned by George Edwards and affectionately known as 'George Edward's Dodo', painted by Roelandt Savery in *c.*1626 (still held in the library of the Natural History Museum [NHM]). The last definite mention of this specimen including the soft tissue was *c.*1848 (e.g. Richardson 1851). The foot was mentioned again by Newton & Gadow (1896) as 'still reposing in the British Museum, but without its integuments'. This suggests that like the Oxford specimen, the London specimen's soft tissue had decayed or been dissected and in fact the foot, as originally depicted in Strickland & Melville (1848), no longer

Figure 4. Oxford foot bones.

existed. Therefore it is likely that today the so-called missing foot (e.g. Fuller 2002) consists only of bone (after being cast) and researchers looking for the soft tissue specimen are, in fact, searching for the wrong type of material. Thus, by the end of the 1800s very little tangible non-fossil Dodo material was available for study.

The Oxford Dodo head was dissected and illustrated in 1847, along with the London foot (Strickland & Melville 1848). The Oxford foot was also dissected, but by this time it lacked most of its soft tissues and, until recently, was never thought to have been illustrated with integuments.

Newly discovered illustrations

During a search of the zoological drawings held at the NHM, London, one of us (AD) discovered a folder entitled '*Didus*' (Linnaeus's second but junior synonym for the dodo) compiled by John Edward Gray (1800–75). Gray joined the staff of the then British Museum (now NHM) as an assistant in 1824, becoming Keeper of Zoology in 1840 until his retirement in 1874 (Anon. 1904). Gray amassed a large collection of published natural history illustrations in scrapbooks and also produced some drawings of his own. The '*Didus*' folder contained one double-sided sheet measuring 340 × 210 mm with illustrations in black ink on paper bearing an 1824 watermark (Figs. 1–2). Gray presented these dodo illustrations to the Zoological Club of the Linnean Society on 24 April 1828 (Anon. 1828) and, therefore, the pictures must have been executed during this four-year period. A short note was published and this is the only mention made of Gray's dodo sketches we have managed to trace:

'At the request, of the Chairman, Mr. Gray exhibited a sketch of the foot of the dodo, *Didus ineptus*, L., [*Raphus cucullatus*] preserved in the British Museum, and another sketch of that contained in the Ashmolean Museum of Oxford, and also a head remaining in the latter collection. He remarked that the feet agreed so perfectly



Figure 5. Dissected Oxford head.

in characters as to leave no doubt of their having belonged to the same species, but that although they were of opposite sides, the one being left and the other right, they must have been obtained from different individuals, the Oxford specimen being one inch shorter than that of the British Museum.'

On one side of the drawings is illustrated the Oxford head in dorsal and lateral views (Fig. 1) whilst the other side illustrates, uniquely, the Oxford and London dodo feet (Fig. 2), with accompanying annotations including measurements. On the first sheet accompanying the dodo feet the following measurements are presented:

Oxford Specimen. Length a. Right foot Length. 8 inches & half from joint to end of middle toe Museum [London] Specimen. B. left foot Length. 9 inch and a half.

On the second sheet accompanying the dodo head drawings the following notes are made: [dorsal view, left] *4 inches* [across head], *2.1/4* [in front of eyes], *1.1/4* [across tip of bill]. [lateral view, right]; *nakedish with scattered hairs ending in two or three heads* [written on head]; *cere naked hard skin* (in the middle); *cover of this part is thin. horny. the bone solid. porous* [on bill tip]

Whilst examining Sir Richard Owen's correspondence in the same library, JPH found a hitherto unpublished illustration of a Dodo head. The watercolour is signed 'WC' (William Clift, 1775–1849, conservator of the Hunterian collection, London) and comprises an illustration of the head of the Oxford Dodo specimen prior to its dissection (Fig. 3). Of particular note in this illustration is the presence of many head feathers that have subsequently disappeared. The discovery of Gray's previously unpublished illustrations constitutes the only scientific documentation of all known skin specimens of the Dodo illustrated together. This is particularly important for comparative study.

Discussion

Based on the handwritten measurements by Gray, the Oxford right foot is *c.*11% smaller and more gracile than the London left foot, yet the tarsometatarsus bone of the Oxford foot has fully-fused epiphyses, indicating the animal to be adult (Fig. 4). Such a size discrepancy in a Columbiform has been interpreted as representing sexual dimorphism (Livezey 1993). Gray's illustration certainly indicates that the London foot is larger than the Oxford foot, but virtually nothing is known of dodo ecology. Therefore, any interpretations based on these drawings must be made cautiously.

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How confident are we that a species is extinct? Quantitative inference of extinction from biological records

David L. Roberts & Anna Saltmarsh

In most cases, the extinction of a species is not directly observed and must instead be inferred from the record of sightings or collections of individual organisms. It is common in such cases to date extinction to the time of the last sighting. However, when a species becomes rare prior to extinction, it may exist for many years without detection and the time of last sighting can be a poor estimate of the time of extinction (Roberts & Solow 2003). Until recently, a species was regarded as extinct if it had not been observed for 50 years (Reed 1996). However, the usefulness of this criterion is dependent on the life-history characteristics of the species in question. A revision of the IUCN Red List categories resulted in a species being classified as Extinct only when exhaustive surveys failed to produce any observations over a time period appropriate to the species' life history and throughout its known historical range (IUCN 2001). However, such quantitative assessments of trends in range and abundance are costly, requiring extensive field studies over a long period of time (Burgman *et al.* 2000).

Two types of sightings data may be available, (a) field observations and (b) data available for specimens, of which there are estimated to be *c.* 2.5 billion specimens in biological collections (Suarez & Tsutsui 2004). Unlike *in situ* sightings, these records represent primary verifiable observations and are built directly on current taxonomic expertise. Such collections represent, for the vast majority of species, our only knowledge. If we cannot successfully monitor populations for the purpose of conservation assessments, it becomes almost impossible to predict their decline or extinction with any certainty (Roberts & Kitchener 2006). Several methods have been presented which provide a probabilistic basis for the extinction hypothesis using these sighting dates to construct a binary time series record (Solow 1993a,b, Burgman 1995, McCarthy 1998, Solow & Roberts 2003, McInerny *et al.* 2006). Essentially these methods provide the probability that another collection will be made given the characteristics of a time series. Recently, a statistical method (Roberts & Solow 2003), optimal linear estimation, has been used to estimate the actual extinction date.

An illustrated example

Ivory-billed Woodpecker *Campephilus principalis* was once widespread across the south-east United States (nominate *principalis*) with another race in Cuba (*C. p. bairdii*) (Short 1982, Collar *et al.* 1992, 1994, Fuller 2001). However, between the 19th century and 1930s it experienced a dramatic decline due to forest clearance (Fuller 2001). The species' requirement for large tracts of virgin forest was partially

its downfall, as it had large territory requirements (Collar *et al.* 1994) with a maximum abundance of one pair per 16 km² (Tanner 1942, King 1978–79), with further data suggesting that the density was even lower (Collar *et al.* 1992). In addition, commercial collection may have played a part in the decline of the species (Collar *et al.* 1992), along with competitive interaction with Pileated Woodpecker *Dryocopus pileatus* (Short 1982). Much of our knowledge stems from the survey of James T. Tanner in the 1930s, when he found only a few individuals (Tanner 1942). At the time, hope for the survival of the species centred on the 80,000-acre Singer Tract in Louisiana (Collar *et al.* 1992). However, the last sighting in this area was in 1944 (Fuller 2001), and the population probably disappeared by 1948 when the remaining 311 km² were cleared (King 1978–79). The last authentic sighting in the United States of Ivory-billed Woodpecker occurred in the Apalachicola Swamp of Florida in 1952 (Fuller 2001). Many now regard the species as probably extinct (Short 1982, Collar *et al.* 1992, 1994).

Based on ten sightings in 1928–52 (1928, 1929, 1935, 1936, 1937, 1938, 1939, 1941, 1944, 1952) (E. Fuller pers. comm.) we can estimate the extinction date using the method described by Roberts & Solow (2003) to $\hat{\theta} = 1969$, eight years after the last sighting. The approximate 0.95 confidence interval for θ is (1958, 1991). The width of this confidence interval is a result of the low sighting rate at the end of its sighting record.

Reports still occur, but no verifiable evidence has been produced. It is thought that many of these sighting may be of the similar, but smaller, Pileated Woodpecker (Fuller 2001). Although the two species are easily distinguished, it is human nature to want to see the rarer of the two. In the case of the Thylacine, recent sightings have largely been disproved, in fact the distance at which an encounter is made can be doubled and the duration of the sighting halved (Anon. pers. comm.).

Discussion

Application of statistical methods for inferring extinction from sightings records and museum specimens will aid our understanding of the probability of whether a taxon has become extinct. However, inference of extinction based on sightings is difficult, largely due to the inference that can be drawn from a sighting record that is dependent on how the sighting rate varies. As with other types of ecological data, interpretation of sightings data requires an understanding of the underlying processes (Solow & Roberts 2003).

Postscript: Avian resurrection

It is almost impossible to determine with certainty whether a species is extinct. The apparent rediscovery of Ivory-billed Woodpecker in 2004 is certainly remarkable, as it had been consigned to the list of North America's Extinct or 'Probably Extinct' bird species (Fitzpatrick *et al.* 2005, 2006), although the rediscovery has been thrown into question (Nemésio & Rodrigues 2005, Jackson 2006, Sibley *et al.*

2006). However its rediscovery, after more than 50 years, begs the question how do we know when a species is extinct? (Roberts in press)

We described above how a sighting record may be used to give a probabilistic basis to an extinction statement. However, we used the $k=10$ most recent sightings of the Ivory-billed Woodpecker to determine a possible extinction date. Using the method described by Roberts & Solow (2003), we estimated the extinction date to be $\hat{\theta} = 1960$, with an approximate 0.95 confidence interval for θ is (1958, 1991). Although not significant in the traditional sense (95%), the extinction statement would still warrant further investigation. However, the model used assumes that the sightings are in the tail of the record, i.e. towards the end of the decline (Coles 2001). In this case they are not; one only needs to examine the high sighting rate particularly during the 1930s. If the $k=5$ most recent sightings prior to its rediscovery in 2004 are used (1938, 1939, 1941, 1944, 1952) the estimated extinction date is $\hat{\theta} = 1969$, with an approximate 0.95 confidence interval for θ is (1958, 2156).

The Roberts & Solow (2003) method was adapted to calculate the significance level (or P -value) in testing the extinction hypothesis as the upper bound of an approximate $1-\alpha$ confidence interval for an unknown time of extinction, T_E (Solow 2005). Roberts (in press) used this to examine the extinction hypothesis for the Ivory-billed Woodpecker in 2004 based on the $k=5$ most recent sightings (1938, 1939, 1941, 1944, 1952). Further, if the Solow & Roberts (2003) non-parametric test is used, both generate probability values greater than 0.05 (0.186 and 0.133 respectively) and thus infers that the species should not have been considered extinct. If we take the last sighting to be 1944 as others have suggested (J. Jackson pers. comm.), then the significance levels are 0.056 (Roberts in press) and 0.047 respectively. Although the latter may be considered not significant in the traditional sense, it would warrant further investigation.

Finally, methods that are based on optimal linear estimation are a good choice for such analysis (Solow 2005). However, the choice of size of k , as seen here, is problematic, too large and it violates the assumption of extreme order statistics, too small and the power is low (Coles 2001). Based on experience, Solow (2005) suggested that when k is at least 5, the method works well.

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Abstracts

Extinction on islands through natural, non-human causes

Storrs L. Olson

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Only in the past quarter century has the true extent of human-caused extinction of birds on islands begun to be realised through great improvements in the fossil record. The global, human-induced catastrophic event on islands has overshadowed the fact that natural factors, such as rising sea level, climate change, volcanism, etc., have also caused extinctions of numerous populations of insular birds in the absence of human influence. Examples, with emphasis on the geological history of Bermuda, will be reviewed with a view towards understanding the effects of past natural events on historically known insular biotas and in an effort to project what the effects of combined natural and human perturbations may have on insular extinction rates in the future.

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New approaches to studying avian extinction events

Alan Cooper, Eske Willerslev & James Haile

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Recent developments in the study of ancient DNA have revealed how genetic traces are often preserved in sediments of sites, even in the absence of macrofossil remains. Whilst we are still unsure of the exact nature by which the DNA is deposited, the records provide a means to examine faunal diversity through time, as well as species prevalence as extinction events are approached. We will present data from studies of New Zealand cave sites, where two volcanic tephra alter the local ecology and moa species diversity in the area.

New molecular analytical methods also make it possible to estimate evolutionary rates, and population sizes of species through time, simply using DNA sequences from dated specimens. This powerful new approach is far more appropriate than the use of external fossil calibration points, which can generate very inaccurate molecular rate estimates. These methods have been used on Beringian bison to demonstrate a large climatic effect in the run-up to the megafaunal mass extinction event. Such an approach would be equally applicable to studies of avian extinctions.

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Using ancient DNA to detect the causes of extinction and endangerment in island birds

Robert C. Fleischer

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Pacific island avifaunas have suffered far higher levels of extinction than any others because of direct and indirect human impacts. Waves of extinction have occurred subsequent to both Polynesian and Western contacts, reducing avifaunas by as much as 60%. It is important to understand how these massive extinctions occurred, and how we can prevent additional extinction of currently endangered species. DNA analyses can contribute to this understanding in a number of ways. First, ancient DNA analyses of extinct and endangered species allow the delineation of units for conservation, and the limits of prior ranges for reintroduction. Comparison of genetic variation in ancient and current populations can be used to estimate effective population sizes and changes in effective population size over time. Use of ancient DNA, in concert with radiocarbon dating, can determine whether the impacts of introduced species, such as the domestic pig, were modified by secondary introductions. Last, ancient DNA can be useful in understanding the timing and impacts of introductions of introduced diseases in Hawaii (e.g., avian malaria, *Plasmodium relictum*), and its vector (a *Culex* mosquito), and how the disease and vector may have changed genetically over time.

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Discovered and lost within 20 years: the story of the Aldabran Brush Warbler

Robert Prys-Jones

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The Aldabran Brush Warbler *Nesillas aldabrana* was discovered in late 1967/early 1968, when a male, female, nest and three eggs were collected on Aldabra Atoll, Indian Ocean, during a year-long Royal Society expedition. The species was not seen again until 1974, in which year RP-J began a two-year field study of a population of c.6 individuals, four of which were colour-ringed. The last sighting, of a colour-ringed individual, was in 1983, and the species now appears almost certainly extinct. The presentation will review knowledge of the biology of *N. aldabrana* and of its status as a species distinct from other *Nesillas* taxa. The limited data available on the ecology of *N. aldabrana* itself will then be considered in conjunction with analogous data from other, better-known Indian Ocean island passerines in order to assess the probable cause(s) of its demise.

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Time since speciation and extinction risk in the western Indian Ocean island avifauna

Ben Warren

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Van Valen (1973) was the first to propose a hypothesis providing theoretical explanation for the observation that the probability of a species becoming extinct is approximately independent of its length of existence. This observation is based on taxonomic survivorship curves compiled from the fossil record. Examination of the molecular phylogenetic placement of extinct and threatened forms of western Indian Ocean *Foudia*, *Zosterops* and *Hypsipetes* reveals an interesting pattern; contrary to Van Valen's (1973) theory, these forms tend to be the oldest members of their clade. This observation is made on the assumption that the mtDNA-based divergence time of a species from its closest relative is representative of its age. Here I test the statistical significance of this apparent trend and discuss possible explanations and the problems that undocumented extinction events present in drawing conclusions.

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